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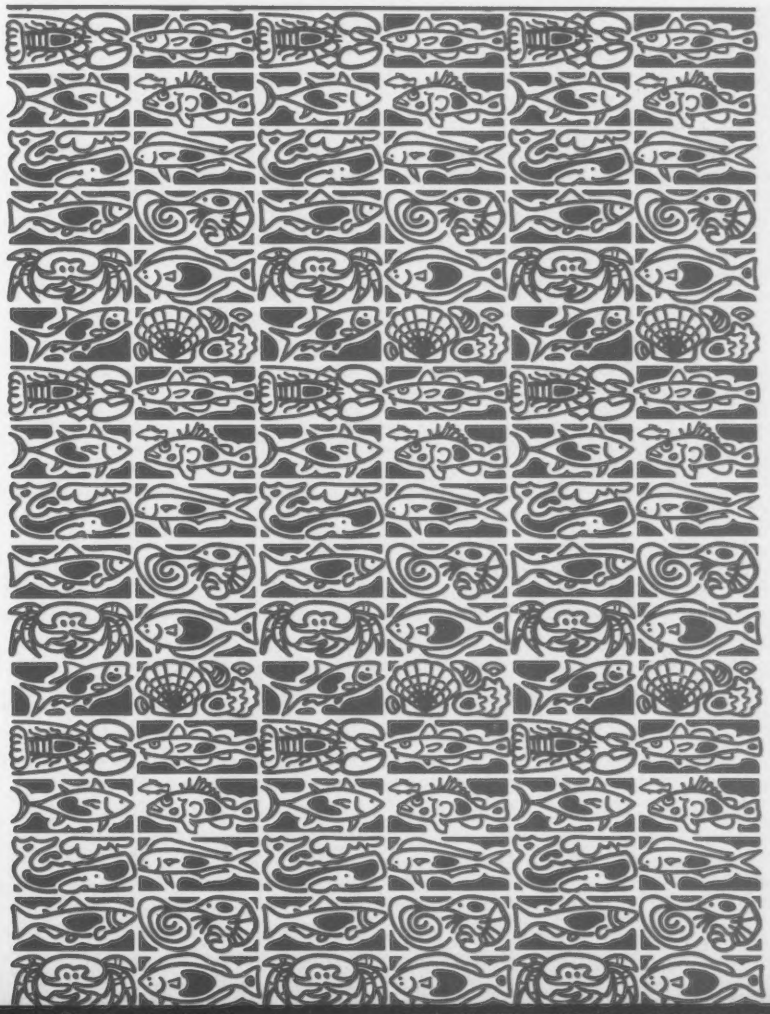

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Demographic variability in seafood consumption rates among recreational anglers of Santa Monica Bay, California, in 1991–1992

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Abstract.—Contaminated fish in Santa Monica Bay, California, have raised concerns about health risks from local seafood consumption. In preparation for a new health risk analysis, a field study was undertaken to determine local angler consumption rates, consumption characteristics, and angler catch. During 1991–92, biologists interviewed 1,244 anglers on piers, party boats, private boats, and beaches; 555 provided consumption-rate estimates. In contrast to previous studies, non-English as well as English speaking anglers were interviewed. The median seafood consumption rate of 21 g/day for local anglers was less than the national average. Consumption-rate distributions were highly skewed, upper-decile consumption rates being several times higher than median rates. Upper-decile consumption rates were more useful than median rates in delineating demographic and species-specific differences in consumption rates. Angler consumption rates of potentially contaminated species and angler awareness of health risks varied by ethnic group; therefore communication of health risks should target habits and languages of high-risk anglers.

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Fishery Bulletin 94:597–610 (1996).

State and Federal regulatory agencies currently use seafood consumption rates in evaluations of health risks from contaminated seafood organisms (Murray and Burmaster, 1994). The United States Environmental Protection Agency (USEPA) estimates that United States recreational anglers consume a median of 30 g/day of fish and shellfish from national waters (USEPA, 1990). Regional medians range from 26 to 37 g/day (Puffer et al., 1981, 1982; Landolt et al., 1985, 1987; Humphrey, 1988; Murray and Burmaster, 1994; SDCDHS[1]). However, extrapolation of national or nonlocal rates to local angling populations can underestimate health risks (Humphrey, 1988). Consumption rates may vary between studies because angler populations differ demographically and in species preference or because rate-determination methods differ. In this study we examine the influence of variability in angler demography, species preference, and rate-determination

[1] SDCDHS (San Diego County Department of Health Services). 1990. San Diego Bay health risk study. Report prepared for Port of San Diego, San Diego, CA. San Diego County, Dep. Health Serv., San Diego, CA, 322 p.

method on seafood consumption rates in a diverse local angling population in Santa Monica Bay, California.

Santa Monica Bay is an embayment of the southern California coast that borders the Los Angeles metropolitan area, one of the largest urban areas in the United States. The presence of chemically contaminated seafood organisms in Santa Monica Bay has raised public concern about the health risk of eating seafood species caught in the Bay (Pollock et al.[2]; SCCWRP et al.[3], SCCWRP[4]). In particular, white croaker, *Genyonemus lineatus*, a species commonly caught by local recreational anglers, is contaminated in some areas of the Bay (Pollock et al.[2]; SCCWRP et al.[3]). Warnings advising restricted consumption of white croaker have been posted since 1985 (Stull et al., 1987; Pollock et al.[2])

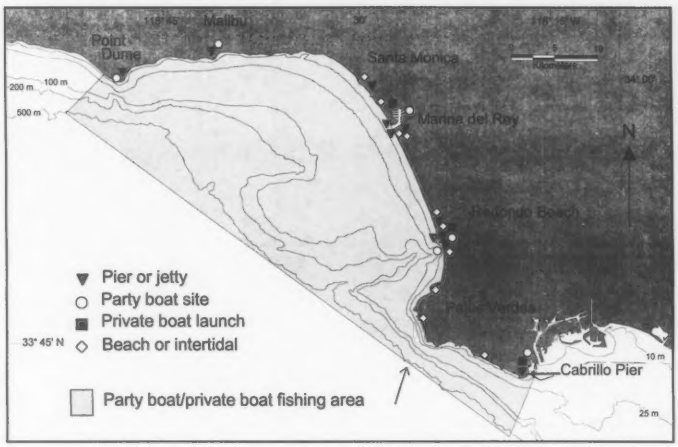

Figure 1

Recreational angler fishing sites sampled in the Santa Monica Bay Seafood Consumption Study, September 1991 to August 1992.

The only study of angler seafood consumption habits for the Los Angeles metropolitan area (including Santa Monica Bay) was conducted in 1980 (Puffer et al., 1981, 1982). The study surveyed more than 1,000 anglers but interviewed only those that spoke English. The median consumption rate of Los Angeles anglers in that study was higher (37 g/day) than the national median (which was 18.7 g/day) (Puffer et al., 1981).

Considering contaminant levels in fish collected in 1987, the State recommended restricted consumption of some species at certain fishing sites in southern California (including Santa Monica Bay) (Pollock et al.[2]). In anticipation of a new risk analysis for the area,[5] a study of seafood consumption habits of Santa Monica Bay recreational anglers was conducted in the early 1990's.[6] The objectives of this study were to describe the demographic and consumption characteristics of Santa Monica Bay anglers, to identify groups with high consumption rates, and to determine the most abundantly caught and consumed species in the early 1990's.

Materials and methods

Field survey

The study area consisted of Santa Monica Bay and adjacent areas, extending from Point Dume to Cabrillo Pier (Fig. 1). It included waters inshore of the 500-m isobath from Point Dume to Cabrillo Pier. We conducted 113 field survey trips at 29 sites on 99 days from 3 September 1991 to 30 August 1992. Interviewers surveyed anglers at piers and jetties (11 sites), party boats (5 sites), private boats (3 sites), and beach and intertidal zones (11 sites) (Fig. 1).

Previous studies indicated that more anglers fish during the summer than during the winter (Stull et al., 1987; NFSP, 1992). Thus, we separated the sampling period into summer (September 1991 and June through August 1992) and nonsummer (October 1991 through May 1992) periods. We conducted survey

[2] Pollock, G. A., I. J. Uhaa, A. M. Fan, J. A. Wisniewski, and I. Witherell. 1991. A study of chemical contamination of marine fish from Southern California. II: Comprehensive study. Calif. Environ. Protection Agency, Office Environ. Health Hazard Assess., Sacramento, CA, 393 p. (161 p. + append.)

[3] SCCWRP (Southern California Coastal Water Research Project), MBC Applied Environmental Sciences, and University of California, Santa Cruz, Trace Organics Facility. 1992. Santa Monica Bay seafood contamination study. Report prepared for Santa Monica Bay Restoration Project, Monterey Park, CA. Southern Calif. Coastal Water Res. Project, Long Beach, CA, 179 p.

[4] SCCWRP (Southern California Coastal Water Research Project). 1994. Contamination of recreational seafood organisms off Southern California. *In* J. N. Cross, C. Francisco, and D. Hallock (eds.), Southern California coastal water research project annual report 1992–1993, p. 100–110. Southern Calif. Coast. Water Res. Project, Westminster, CA.

[5] Santa Monica Bay Restoration Project, Monterey Park, CA, is funding this risk-analysis study.

[6] SCCWRP and MBC (1994) (Footnote 9 in the text) provides a detailed account of sampling protocols, analytical methods, and results of this study.

trips to pier-and-jetty, party-boat, and private-boat sites on two week days and two weekend days per month in summer and on one week day and one weekend day per month in nonsummer.

To minimize sampling bias, we used a stratified-random design to schedule and conduct the survey trips. Fishing modes, regions, sites, and sampling times were selected randomly to maximize spatial coverage of the Bay. For each month, we selected a sampling sequence at random for four regions and sites within each region, using a random numbers table; we surveyed each site in the selected sequence. If a site could not be sampled, we sampled the next site on the list. Sampling was conducted without replacement within a month and with replacement between months.

We chose survey-trip times at random for the three major fishing modes. Interviewers surveyed pier-and-jetty anglers in the morning (0800–1200 h), afternoon (1200–1600 h), or evening (1600–2000 h) with roving surveys. They surveyed party-boat anglers on half-day boats within the study area (full-day boats generally fished outside the area) in the morning (0700–1200 h) or afternoon (1230–1730 h). Private-boat anglers were interviewed at boat launches or hoists in the morning (1000–1400 h) or afternoon (1400–1800 h). Interviewers conducted 1-h beach survey trips before pier-and-jetty surveys and conducted 2-h rocky intertidal surveys on randomly selected afternoons (1300–1700 h) during low tides.

Interviewers tried to interview all anglers at a site. However, if too many anglers were present, they systematically selected every second or third angler. Interviewers censused (counted and characterized) anglers at each site and asked all (or a subset of the anglers) questions from a specially designed questionnaire. All interviewers spoke English; at least one interviewer per survey spoke Spanish; and others spoke Vietnamese, Chinese, or Pilipino. They interviewed a designated household head if two or more individuals from a household were present. Interviewers asked anglers 35 questions regarding their background, their fishing history, the types of fish they had eaten, their consumption habits, their methods of preparing fish, their awareness of health risk warnings, and their response to warnings (Table 1). Anglers chose the ethnic-group category best representing their background from a list used in the most recent United States census report (USBC, 1990).

Interviewers identified to species any fish possessed by anglers and measured its fork length to the nearest centimeter. They showed photographs of important species in order to enable anglers to identify other species consumed during the previous month. The species included bocaccio (*Sebastes paucispinis*), barred sand bass (*Paralabrax nebulifer*), kelp bass (*Paralabrax clathratus*), white croaker, queenfish (*Seriphus politus*), California corbina (*Menticirrhus undulatus*), chub (=Pacific) mackerel (*Scomber japonicus*), and California halibut (*Paralichthys californicus*). Interviewers also carried a balsa-wood model of a 150-g generic fish fillet (based on a fillet of that size obtained from a supermarket [the USEPA standard meal size; USEPA, 1989]). They asked anglers to estimate their meal size for each species (in hand or in photographs) in relation to the fillet model. The fillet model gave the angler a three-dimensional image of the standard meal size.

Data analysis

Questionnaire responses were numerically coded and entered into a computer database for analysis. We calculated consumption rates by two methods. The primary method used the angler's estimates of meal size based on a 150-g fillet model. The other method used consumable-portion sizes of fish possessed by an angler. For the latter method, we converted lengths of fish measured in the field to total and consumable-portion weights. These were estimated for each fish from weight-length regressions[7] and from consumable-portion information.[8] In both methods, we multiplied the amount consumed per meal or the consumable portion by the number of times an angler consumed that species during the previous four weeks. This gave a monthly consumption rate (in grams per month). We divided this rate by 28 days to get daily consumption rates (in grams per day). For the consumable-portion method, we divided the consumable portion by the number of consumers in the household. We did not do this for the fillet-model estimates because we obtained only information on the angler's meal size.

Consumption rate data were summarized by parametric (means, standard deviations, and 95% confidence limits) and nonparametric statistics (median and upper decile or 90th percentiles). We tested for consumption-rate differences among ethnic and income groups using a Kruskal-Wallis one-way analysis of variance on ranked data. We tested for differences between fillet-model and consumable-portion estimates of consumption rates using a Wilcoxon's sign-rank test or paired t-test, as appropriate.

[7] S. J. Crooke, Calif. Dep. Fish Game, Long Beach, CA, provided weight-length relationship information.

[8] W. Jacobson, U.S. Dep. Commer., Natl. Ocean. Atmos. Admin., Natl. Mar. Fish. Serv., Los Angeles Reg., Long Beach, CA, provided consumable-portion information.

Table 1

Information collected by a questionnaire administered to recreational anglers during the Santa Monica Bay seafood consumption study, September 1991 to August 1992.

No.	Information
1	Interviewer(s)
2	Date
3	Location
4	Interview time (begin and end)
5	Fishing technique used by angler — hook-and-line (number of poles), other
6	Observed gender of angler
7	Permission or not to interview angler
8	Angler previously or not interviewed for this study
9	Length of time angler fished at location during day of interview (number of hours)
10	Additional time angler expected to fish during day of interview (boat anglers excluded)
11	Number of years or months angler fished in Santa Monica Bay
12	Seasons angler fished
13	Number of times angler fished at location during past four weeks
14	Angler's fishing experience elsewhere in Santa Monica Bay during past four weeks (number of times, fishing mode, site)
15	Number of times angler consumed fish caught in Santa Monica Bay during past four weeks
16	Number of fish caught during day of interview
17	Permission or not to examine angler's catch
18	Species caught:
	a correct species name, angler's name for species
	b fish length (cm)
	c fate of fish (eat, throw back, give away, other)
	d parts of fish consumed (whole gutted, fillet/steak, whole with intestines, other)
	e how much consumed (relative to fillet model)
	f preparation method (fry, broil/barbecue, bake/boil/steam, raw/smoked/ceviche, soup, other)
19	Specific species (shown in photos): (a–f, same as in question 18)
20	Was angler aware of fish consumption health warnings for Santa Monica Bay?
21	How was angler informed of the health warnings (posted signs, TV, newspapers or magazines, anglers/friends, other)?
22	Did angler respond to warnings? (If yes, how? Eat less of all or specific species? Stopped eating all or specific species?)
23	Importance of warnings to angler
24	Angler's town and zip code of residence
25	Angler's occupation
26	Angler's age
27	Angler's racial or ethnic background
28	Number of angler's family members fishing at site that day
29	Others in angler's household: number, ages, participation in and frequency of consumption of catch from Santa Monica Bay, relative amounts eaten (compared with fillet model)
30	Angler's family income
31	Permission to call angler
32	Best time of day to call angler
33	Angler's phone number
34	Angler's name
35	Interviewer observations (quality of interview, survey type, comments, language used in interview)

Results

Angler characteristics and catch

During the survey year, interviewers counted 2,376 anglers and approached 1,740 for interviews. Of those approached, they did not interview 149 (9%) because of language barriers and 347 (20%) because they refused information. They interviewed 1,244 anglers; of these, 555 provided sufficient information for consumption-rate calculations (Table 2). Of these 555 consumers, 232 (42%) were interviewed on party boats, 210 (38%) on piers and jetties, 106 (19%) on private boats, and 7 (1%) at beach and intertidal areas. Hence, we did not consider beach and intertidal areas as a major fishing mode. On the average, they interviewed 52% of the anglers at a site. By mode, the mean percentage interviewed at a site was 59%

Table 2

Sampling success in surveys of recreational anglers by fishing mode and time of week, Santa Monica Bay seafood consumption study, September 1991 to August 1992.

Fishing mode and period	No. survey trips	Anglers						
		Counted	Approached		Interviewed		Used in study	
		No.	No.	%[1]	No.	%[2]	No.	%[3]
Piers								
Weekday	16	313	333	106	221	66	97	44
Weekend	16	571	453	79	299	66	113	38
Total	32	884	786	89	520	66	210	40
Party boats								
Weekday	16	365	264	72	190	72	101	53
Weekend	16	612	366	60	260	71	132	51
Total	32	977	630	64	450	71	233	52
Private boats								
Weekday	16	131	87	66	75	86	29	39
Weekend	16	350	217	62	183	84	77	42
Total	32	481	304	63	258	85	106	41
Beach								
Weekday	8	14	8	57	7	88	5	71
Weekend	5	8	7	88	4	57	1	25
Total	13	22	15	68	11	73	6	55
Intertidal								
Weekday	4	12	5	42	5	100	0	0
Grand total	113	2,376	1,740	73	1,244	71	555	45

[1] % approached = (no. approached/no. counted) × 100; number of anglers approached for interviews was higher than number initially counted when late-arriving anglers on pier were interviewed.
[2] % interviewed = (no. anglers approached/no. interviewed) × 100.
[3] % used in study (i.e. providing consumption information) = (no. used/no. interviewed) × 100.

at piers and jetties, 54% on private boats, 50% on beaches, 47% on party boats, and 42% at beach and intertidal sites.

Santa Monica Bay anglers comprised several demographic groups. Most were males (93%), 21–40 yr old (54%), and white (43%), with annual household incomes of $25,000–$50,000 (39%) (Fig. 2). Anglers were 8–86 yr old and less than 10% were younger than 21 years. Because we interviewed only household heads, we probably underestimated numbers of anglers below 21 years; therefore, we excluded these from the age-frequency summary (Fig. 2). The following ethnic groups were noted: white, black, Hispanic, and Asian (including Japanese, Koreans, Chinese, Filipinos, Vietnamese, Cambodians, Indonesians, Pakistanis, and Pacific Islanders). The second most abundant ethnic group was Hispanic, followed by Asian, and black (Fig. 2). "Others" included a native American, an Iranian, and an Egyptian, as well as anglers not providing ethnic information. Hispanics were the predominant group on piers and jetties, whereas whites were the predominant group on party boats and private boats (Fig. 3). Most (60%) anglers with incomes below $10,000 fished on piers and jetties. Most (46%) anglers had fished 5 yr or less in Santa Monica Bay, whereas 7% had fished more than 30 yr. Most (63%) anglers fished all year but 19% fished only in summer. About (33%) had not fished during the month (28 days) before the interview, but of those that had, most had fished 3–5 times per month and for 2–5 h at a time.

Interviewed anglers possessed at least 67 species of fish, two species of crustaceans, two species of mollusks, and one species of echinoderm from the study area. The most abundant species were chub mackerel, barred sand bass, kelp bass, white croaker,

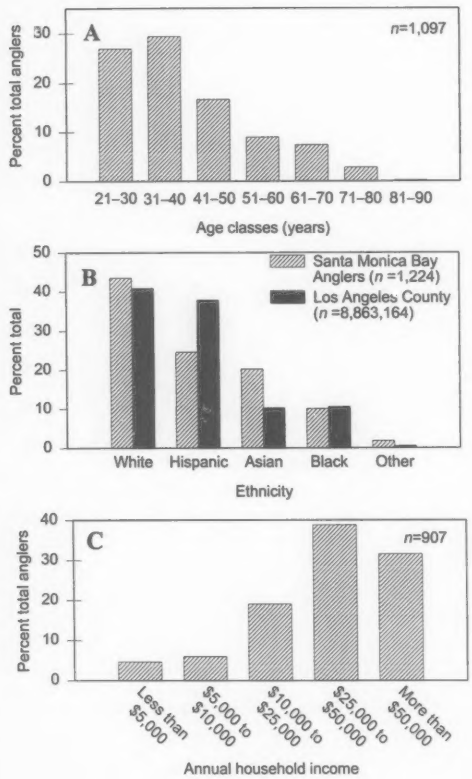

Figure 2

Characteristics of recreational anglers interviewed in the Santa Monica Bay seafood consumption study, September 1991 to August 1992: (**A**) age distribution (anglers older than 20 yr); (**B**) ethnic distribution (anglers and general population of Los Angeles County in 1990 [USBC, 1990]); and (**C**) annual household income distribution (non-respondents not included).

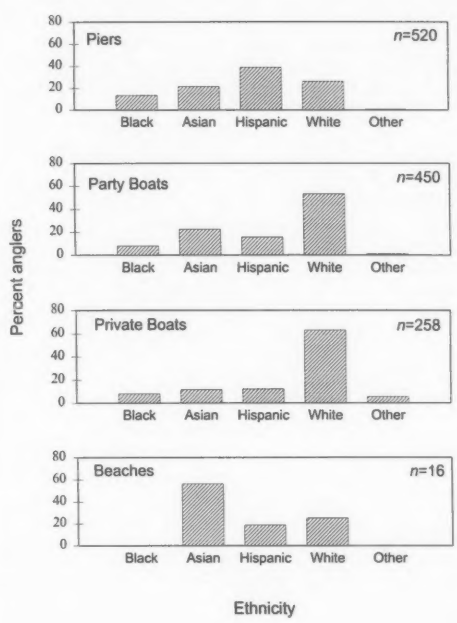

Figure 3

Ethnic distribution of recreational anglers by fishing mode, Santa Monica Bay seafood consumption study, September 1991 to August 1992.

Pacific barracuda (*Sphyraena argentea*), and Pacific bonito (*Sarda chiliensis*) (Table 3). Most anglers could not give the correct common name (Robins et al., 1991) (e.g. Pacific barracuda, chub mackerel) for fish species but generally could give the correct generic common names (e.g. barracuda, mackerel).

Only 45% of the respondents had eaten fish from the Bay within four weeks of the interview, and most anglers had caught fish on the interview day. More party-boat (76%) and private-boat (74%) anglers had caught fish on the interview day than had pier-and-jetty anglers (47%). About 63% of the anglers intended to eat their catch. Private-boat anglers were most likely (70%) and pier-and-jetty anglers least likely (58%) to eat their catch. Pacific bonito, Pacific barracuda, and California halibut were the species most frequently eaten if caught, whereas white croaker, chub mackerel, and queenfish were the species most frequently thrown back.

About 65% of the anglers ate fish steaks or fillets, whereas 33% ate their fish whole but gutted; only 1% ate whole ungutted fish. Whites, blacks, and Hispanics usually ate fish steaks or fillets, whereas Asians ate whole gutted fish with equal frequency. About 47% of the anglers fried their fish, 27% used a variety of cooking methods, and 17% broiled or barbecued their fish. Frying was the most common method of cooking fish for all ethnic groups. However, a combination of methods was important for all groups other than the Hispanic. Broiling and barbecuing was also an important cooking method for whites but less so for the other groups. We did not ask anglers if they consumed fish with or without skin.

Consumption rates

Consumption-rate distributions were strongly right-skewed (Fig. 4). From fillet-model estimates, Santa Monica Bay anglers had a median consumption rate

Table 3

Species most commonly caught by recreational anglers with different fishing modes, Santa Monica Bay seafood consumption study, September 1991 to August 1992.[1]

Common name	Scientific name	Number of organisms				
		Piers or jetties	Party boat	Private boat	Beach or intertidal	Total
chub mackerel	*Scomber japonicus*	476	356	215	0	1,047
barred sand bass	*Paralabrax nebulifer*	1	308	79	0	388
kelp bass	*Paralabrax clathratus*	1	250	76	0	327
white croaker	*Genyonemus lineatus*	167	3	149	0	319
Pacific barracuda	*Sphyraena argentea*	4	202	53	0	259
Pacific bonito	*Sarda chiliensis*	25	124	101	0	250
sea mussel, unidentified	*Mytilus* spp., unidentified	0	0	0	100	100
Pacific purple urchin	*Strongylocentrotus purpuratus*	0	0	0	90	90
jacksmelt	*Atherinopsis californiensis*	64	2	8	0	74
California scorpionfish	*Scorpaena guttata*	3	34	28	0	65
bocaccio	*Sebastes paucispinus*	0	46	16	0	62
California halibut	*Paralichthys californicus*	12	23	27	0	62
halfmoon	*Medialuna californiensis*	0	32	24	0	56
opaleye	*Girella nigricans*	31	0	12	9	52
rockfish, unidentified	*Sebastes* spp., unidentified	0	34	3	0	37
squarespot rockfish	*Sebastes hopkinsi*	0	29	0	0	29
surfperches, unidentified	*Embiotocidae* spp.	18	0	9	0	27
black perch	*Embiotoca jacksoni*	5	0	21	0	26
starry rockfish	*Sebastes constellatus*	0	18	6	0	24
yellowfin croaker	*Umbrina roncador*	16	0	1	3	20
other species combined		95	67	69	11	242
total		918	1,528	897	213	3,556
rockfishes, combined[2]	*Sebastes* spp., combined	4	166	28	0	198

[1] A complete list of observed species is given in SCCWRP and MBC (Footnote 9 in the text).
[2] Rockfishes combined included 15 identified and one unidentified species, some of which (i.e. boccacio, squarespot rockfish, rockfish unidentified, and starry rockfish) are included in the top 20 species shown in this table as separate species and others as other species combined. Because rockfishes are commonly combined in catch summaries, the catch of the group as a whole is also shown separately.

of 21 g/day and an upper-decile rate of 107 g/day (Table 4). Thus about 10% of the anglers had consumption rates more than five times the median (Fig. 4; Table 4).

Consumption rate distributions for ethnic and income groups were also strongly right-skewed. Median consumption rates for ethnic groups ranged from 16 g/day (Hispanics) to 24 g/day (blacks) (Table 4). Although median consumption rates among ethnic groups were not homogeneous (Kruskal-Wallis; H=10.759; df=3; P=0.0131), none differed significantly from each other (Dunn's method). Upper-decile consumption rates ranged from 64 g/day (Hispanics) to 137 g/day (Asians) (Table 4). Although anglers with annual household incomes less than $5,000 had higher median consumption rates (Table 4), these did not differ significantly from the others (Kruskal-Wallis; H=1.776; df = 4; P=0.7768). Upper-decile consumption rates by income group ranged from 48 g/day ($5,000–$10,000) to 129 g/day (>$50,000) (Table 4).

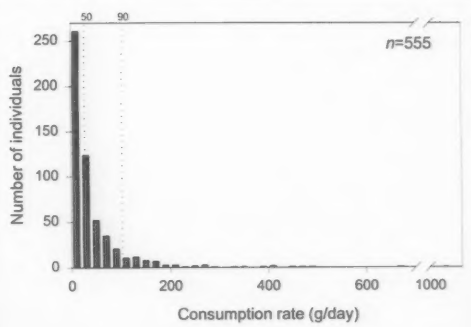

Figure 4

Distribution of seafood consumption rates (all fish species combined) for recreational anglers interviewed in the Santa Monica Bay seafood consumption study, September 1991 to August 1992. Median (50th percentile) and upper decile (90th percentile) are noted with vertical dotted lines.

Table 4

Angler consumption rates of all fish species by ethnic, income, and seasonal groups, Santa Monica Bay seafood consumption study, September–August 1992. CL = ± confidence limit (95%). UD = upper decile (90th percentile).

Category	Number of anglers	Consumption rate (g/day)			
		Mean	CL	Median	UD
Ethnicity[1]					
White	218	58	19	21	116
Hispanic	137	28	6	16	64
Black	57	49	19	24	99
Asian	135	60	20	21	137
Income[2]					
<$5,000	20	42	18	32	64
$5,000–$10,000	27	41	29	21	48
$10,000–$25,000	90	40	9	21	80
$25,000–$50,000	149	47	11	21	113
>$50,000	130	59	21	21	129
Fishing season					
Summer (June–September)	295	55	16	21	113
Nonsummer (October–May)	260	44	8	21	107
Total (all anglers)	555	50	9	21	107

[1] The eight anglers that gave no response to the ethnicity question were not included here. Ethnic categories are those used by USBC (1990).
[2] The 139 anglers that gave no response to the income question were not included here.

Consumption rates of anglers fishing in summer and nonsummer months did not differ significantly (Mann-Whitney rank sum test; T=72,857; n(small)=260; n(large)=295; P=0.7597). Median consumption rates were 21 g/day for both groups (Table 4).

Median consumption rates of the most commonly caught species were similar (11–16 g/day) but upper-decile rates were more variable (27–80 g/day) (Table 5). Some individuals greatly exceeded average consumption rates for chub mackerel (Fig. 5). Median consumption rates were highest (16 g/day) for barred sand bass, kelp bass, combined rockfish species (*Sebastes* spp.), Pacific bonito, Pacific barracuda, and California halibut (Table 5). Upper-decile consumption rates were highest for kelp bass, barred sand bass, and combined rockfishes (80, 78, and 63 g/day, respectively). Rates of consumption of specific species varied by ethnic group (Table 5). Species with highest median and upper-decile consumption rates, respectively, by ethnic group were as follows: jacksmelt, *Atherinopsis californiensis*, and barred sand bass (white); barred sand bass and chub mackerel (Hispanic); rockfishes and chub mackerel (Asian); and Pacific bonito and California halibut (black).

Consumption rates estimated by the fillet-model and by the consumable-portion methods did not differ significantly for all species, chub mackerel, or kelp bass (Table 6). However, consumable-portion estimates were significantly higher for barred sand bass, Pacific bonito, Pacific barracuda, and California hali-

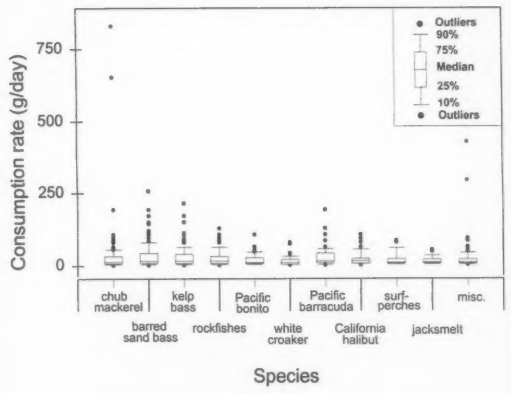

Figure 5

Seafood consumption rates (by fish species) for recreational anglers interviewed in the Santa Monica Bay seafood consumption study, September 1991 to August 1992.

Table 5

Consumption rates (g/day) by fish species for Santa Monica Bay anglers of different ethnic groups, September 1991 to August 1992. *n* = number of anglers. Md = median (50th percentile) consumption rate in g/day. UD = upper decile (90th percentile) consumption rate in g/day.

	White			Hispanic			Asian			Black			All[1]		
Fish species	*n*	Md	UD	*n*	Md	UD	*n*	Md	UD	*n*	Md	UD	*n*	Md	UD
chub mackerel	31	16	48	53	12	43	49	16	98	12	11	24	147	13	54
barred sand bass	72	19	86	20	16	32	35	11	54	16	16	58	144	16	78
kelp bass	75	16	55	14	11	37	34	12	80	16	19	64	140	16	80
rockfishes	50	16	43	13	8	24	28	23	64	10	16	32	101	16	63
Pacific bonito	24	11	30	23	11	36	23	11	44	4	28	54	77	11	44
white croaker	10	11	11	41	11	32	5	5	51	14	13	37	72	11	32
Pacific barracuda	42	21	54	8	11	36	16	11	55	4	24	79	71	16	54
California halibut	39	11	43	5	11	23	9	11	26	8	21	86	62	16	51
surfperches	7	21	44	4	11	14	6	11	32	3	8	59	20	11	27
jacksmelt	5	32	40	9	8	11	5	11	40	4	16	21	23	11	32

[1] Individuals giving no response to the ethnicity question were included in "All" but were not treated as a separate group.

Table 6

Results of Wilcoxon signed-rank test comparing angler seafood consumption rates estimated with fillet-model and consumable-portion methods, Santa Monica Bay seafood consumption study, September 1991 to August 1992. *n* = number of samples. T_s = smaller sum of ranks. *W* = difference between sums of ranks.

		Median consumption rate (g/day)		Absolute value		
Species	*n*	Fillet-model	Consumable-portion	T_s	*W*	*P*
chub mackerel	62	10.7	10.7	844	265	0.3547
barred sand bass	46	10.7	18.6	322	437	0.0017
kelp bass	55	10.7	11.8	729	82	0.7344
rockfish spp.	49	8.2	2.1	294	637	0.0016
Pacific bonito	33	10.7	22.5	90	381	<0.0001
white croaker	29	10.7	2.5	78	279	0.0027
Pacific barracuda	35	10.7	26.1	76	478	<0.0001
California halibut	6	10.7	55.7	0	21	0.0313
surfperch spp.	13	8.2	2.1	0	91	0.0017
jacksmelt	14	9.3	2.1	14	77	0.0171
all species[1]	406	10.7	8.2	40,639	1,343	0.7767

[1] Includes the above species and additional single species with both fillet-model and consumable-portion estimates.

but, and significantly lower for rockfishes, white croaker, surfperches, and jacksmelt.

Overall consumption rates were estimated for anglers with fish and for anglers that had consumed a species shown in a photograph during the previous month (Tables 4 and 5). However, consumable-portion estimates included only anglers with fish. Hence, fewer (406) anglers provided information for both estimates (Table 6). In addtion, we compared only individual species that had both consumable-portion and fillet-model estimates. Hence, the overall median (Table 6) was lower than the overall consumption rate according to all species consumed by an angler during the month (Table 4).

Health concerns

Anglers who consumed white croaker, a potentially contaminated species, were mostly male (92%), Hispanic (57%), 21 to 30 years old (26%), and with household incomes of from $10,000 to $25,000 (17%) (Fig. 6). Although more Hispanics consumed white croaker, blacks had the highest median (13 g/day) and Asians the highest upper-decile (51 g/day) consumption rates of this species (Table 5). Most anglers caught white croaker at piers (particularly Cabrillo Pier), fished all year, had fished less than six years, and had eaten this species at least once during the past four weeks. They generally ate the fish whole but gutted, ate about 150 g at a time, and generally fried their catch.

About 77% of anglers were aware of health warnings regarding consumption of Santa Monica Bay fish, most respondents citing television and newspaper or magazine articles as the major source of these warnings (Table 7). Of the anglers who were aware, 50% had altered their seafood consumption habits. The greatest percentage (46%) of these had stopped consuming some species. Most anglers of all ethnic groups were aware of the warnings. Black and Hispanic anglers generally became aware via television, whereas newspapers and magazines were the major source of health warnings for Asian and white anglers. Most Asian and white anglers altered their consumption behavior, but most black and Hispanic anglers did not. Of those responding, the pattern was similar for all ethnic groups: most stopped eating some species and somewhat fewer ate less of all species. White croaker consumers generally became aware of health warnings from a variety of media sources. Although most thought the warnings were very important, half did not alter their consumption habits (Fig. 7).

Discussion

Santa Monica Bay anglers in the early 1990's included relatively more whites and Asians and fewer Hispanics than the overall Los Angeles County popu-

Table 7

Response to health-risk awareness warnings by recreational anglers of different ethnic groups, Santa Monica Bay seafood consumption study, September 1991 to August 1992.

	Ethnic group					
Concern	Black	Asian	Hispanic	White	Other	Total
Number of respondents						
Total number	124	251	306	541	22	1,244
Number aware of warnings	95	185	179	473	10	942
Number affected by warnings	43	104	78	244	3	472
Warning awareness (percent respondents)						
Percent aware	77	74	58	87	45	76
Percent not aware/no response	23	26	42	13	55	24
Source of warnings (percent of aware)[1]						
Percent by television	61	46	64	51	20	53
Percent by newspaper or magazines, or both	45	47	30	58	30	49
Percent by posted signs	33	38	32	31	60	33
Percent by anglers or friends, or both	20	19	14	27	20	22
Percent by other	6	10	7	12	10	10
Response to warnings (percent of aware)						
Percent affected by warnings	45	56	44	52	30	50
Percent not affected	55	44	56	48	70	50
Type of response (percent of affected)						
Percent stopped eating some species	37	52	44	46	0	46
Percent ate less of all species	37	26	28	20	67	25
Percent stopped eating all species	19	13	18	21	0	19
Percent ate less of some species	7	9	10	12	33	11

[1] Respondents could say "yes" to more than one category; hence, percentages may sum to more than 100%.

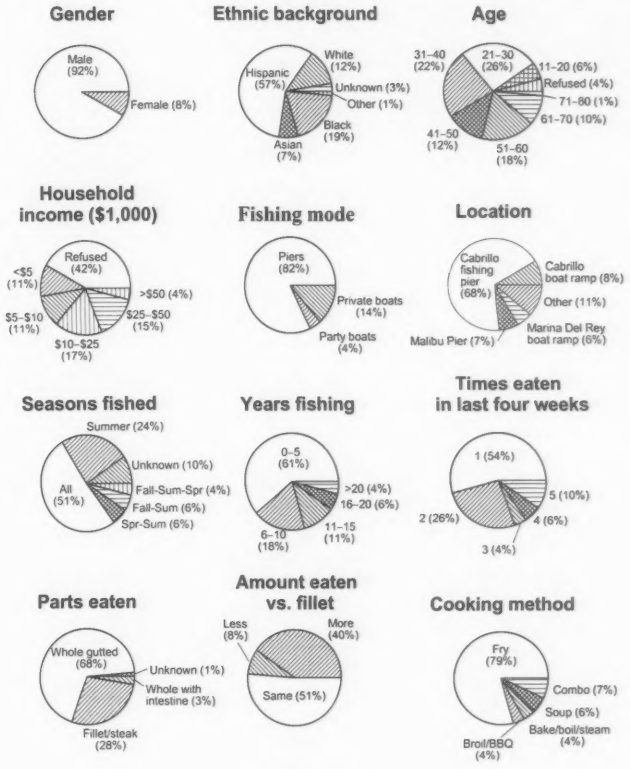

Figure 6

Characteristics of recreational anglers who consumed white croaker, *Genyonemus lineatus*, in the Santa Monica Bay seafood consumption study, September 1991 to August 1992. Sample size = 72 anglers.

lation (Fig. 2) (USBC, 1990; SCCWRP and MBC Applied Environmental Sciences[9]). Surprisingly, the gender, age, and ethnic characteristics of Santa Monica anglers in 1991–92 had not changed much since 1980 (Puffer et al., 1981, 1982).

Santa Monica Bay anglers commonly caught white croaker, chub mackerel, and Pacific bonito in 1980 (Puffer et al. 1981, 1982) and 1991–92. However, they caught fewer white croakers in 1991–92. Local anglers in 1991–92 caught similar species to southern California anglers in 1989, who primarily caught barred sand bass, Pacific bonito, and chub mackerel (NFSP, 1992). In all three surveys, similar survey methods were used and anglers were interviewed at piers and jetties, party boats, and private boats.

In seafood consumption studies, estimated rates are commonly based on consumable portions (Puffer et al., 1981, 1982; Landolt et al., 1985, 1987; SDCDHS[1]). However, in some studies (e.g. Murray and Burmaster, 1994) fillet-model estimates have been used. Of the two methods, we preferred the fillet-model method because the angler gave specific information on meal size. With the consumable-portion method, the number of household consumers influenced the estimated meal size. With consumable-portion estimates, we assumed that household consumers would eat the entire consumable portion and would catch similar-size fish on other fishing days. This resulted in unreasonably high estimates for large and less

[9] SCCWRP (Southern California Coastal Water Research Project) and MBC Applied Environmental Sciences. 1994. Santa Monica Bay seafood consumption study. Report prepared for Santa Monica Bay Restoration Project, Monterey Park, CA. Southern Calif. Coastal Water Res. Project, Westminster, CA, 199 p. (101 p. + appendices.)

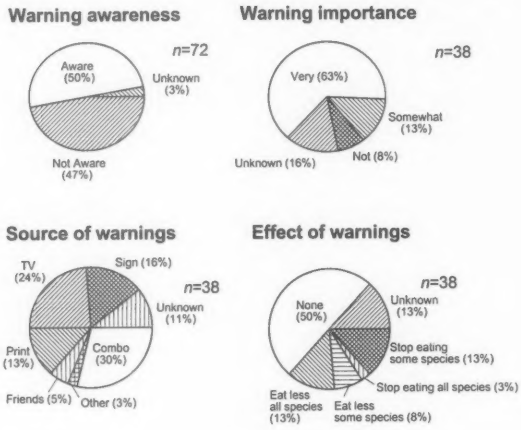

Figure 7

Responses to health risk warnings by Santa Monica Bay anglers who consumed white croaker, *Genyonemus lineatus*, in the Santa Monica Bay seafood consumption study, September 1991 to August 1992.

abundant species (e.g. California halibut). Consumable-portion method estimates were generally higher than fillet-model estimates for larger species and lower for smaller species. With the consumable-portion method, estimated rates were calculated only for species in an angler's possession at the time of the interview. In contrast, the fillet-model method also provided consumption-rate estimates for species not caught on the interview day.

Fillet-model medians varied less between species than did consumable-portion medians (Table 6) because the fillet-model method used fewer measurement units for meal size. The angler estimated meal size in relation to the model size (e.g. 0.5, 1.0, or 2.0 times the model). Thus, if the angler consumed a meal equal in size to the model twice a month, his or her consumption rate would be 10.7 g/day. The consumable-portion medians were more variable, in part because the consumable-portion weights had more divisions (i.e. grams).

Consumption-rate distributions were strongly right-skewed. Hence medians and upper-deciles provided more appropriate summaries than did arithmetic means and 95% confidence limits. The skewed distributions indicate that relatively few anglers had high consumption rates, whereas many had low consumption rates. All demographic groups examined had right-skewed consumption-rate distributions. This was true for all species or individual species. Similar consumption-rate distributions for Michigan anglers were lognormal (Murray and Burmaster, 1994). An upcoming paper[10] will describe statistically the consumption rate distributions from the present study.

In 1989, southern California anglers took 1.85, 1.66, and 1.13 million fishing trips on piers and jetties, private boats, and party boats, respectively (NFSP, 1992). Percentages of total anglers by fishing mode (piers, private boats, and party boats, respectively) were 40, 36, and 24% in 1989 and 42, 21, and 37% in the present study. Pier anglers represented about the same percentage of the population in both surveys. However, the present study differed in having more party-boat than private-boat anglers. Thus, there may be relatively fewer private-boat anglers in Santa Monica Bay than in southern California as a whole. Because the NFSP estimates were from fishing trips, some anglers may have repeated trips. Hence, the trips do not accurately represent the numbers of different anglers (which we needed for consumption rates).

We used only data collected in our study to calculate consumption rates. Where we summarized data for the whole study population, we combined data for each fishing mode (i.e. piers, party boats, and private boats). We did not adjust these estimates for

[10] Hill, M. D., and D. M. Lee. 1996. Estimated distributions of average daily fish consumption rates among Southern California marine anglers. Calif. Environ. Protection Agency, Sacramento, CA. In prep.

possible differences in numbers of anglers using each mode. We did not know how many anglers annually used each mode and could not estimate the numbers without conducting a special study. However, some weighting occurred naturally owing to the different numbers of anglers fishing (and hence being interviewed) in each mode. Given the limitations and available resources of the study, we believe that this natural weighting provided the best estimate of angler population size for each mode.

The median consumption rate (21 g/day) for Santa Monica Bay anglers was 70% of the national median of 30 g/day (USEPA, 1990). Only 45% of the anglers provided sufficient information for determination of consumption rates. Thus, relatively fewer Santa Monica Bay anglers may rely on their catch as a major food source. In 1980 the median consumption rate of Los Angeles anglers (estimated by the consumable-portion method) was higher (37 g/day) than the national median (which was 18.7 g/day) (Puffer et al., 1981). In that study, upper-decile consumption rates were 225 g/day; upper-decile consumption rates in this study were 107 g/day. Thus, seafood consumption rates among local anglers have decreased substantially (median 43% and upper-decile 52%) since 1980. This may be the result of health-risk warnings (posted since 1985) regarding DDT and PCB contamination of some species (Stull et al., 1987).

Santa Monica Bay anglers generally consumed the most commonly caught species at the highest rates. These species included barred sand bass, Pacific barracuda, kelp bass, combined rockfish species, and California halibut, all of which have low PCB and DDT levels (Pollock et al.[2]; SCCWRP et al.[3]). However, anglers also consumed white croaker at relatively high rates even in areas where it has high levels of PCB and DDT (Pollock et al.[2]; SCCWRP et al.[3]; SCCWRP[4]). Hispanic anglers were the primary consumers of white croaker, commonly catching it at Cabrillo Pier (where it is contaminated) (Pollock et al.[2]). However, although more Hispanics consumed white croaker, blacks and Asians had higher consumption rates for this species.

Although current advisories warn anglers not to consume white croaker in Santa Monica Bay and Los Angeles–Long Beach Harbor (Pollock et al.[2]), clearly many anglers still eat this species. Many anglers aware of the warnings did not alter their consumption rates, reasoning that if there was a health risk, they would experience ill effects within a day of eating the fish. Thus, agencies should improve communication of the risks by using a variety of media and languages. For Santa Monica Bay they should communicate risks in English and Spanish (at minimum) via television, newspapers and magazines, and posted signs, emphasizing piers and private boat launches where anglers catch white croaker for consumption.

Conclusions

In 1991–92, median seafood consumption rates for Santa Monica Bay anglers were lower than the national median. Consumption-rate distributions were skewed strongly to the right; upper-decile rates were often considerably higher than medians. Upper-decile rates varied more among demographic groups and species than did median rates; thus upper-decile rates are valuable in identifying high-risk groups. Overall, Asian and high-income anglers had the highest upper-decile consumption rates. Certain ethnic groups consumed more of the potentially contaminated species (e.g. white croaker). The lack of a strong response to health warnings by anglers indicates that health advisories should communicate the health risks from eating contaminated fish to specific ethnic groups at high-risk sites. Overall, consumption rates determined by consumable-portion and fillet-model methods were similar, but some species-specific rates did differ.

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The use of minisatellite DNA variation for stock identification of chum salmon, *Oncorhynchus keta*

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Abstract.—Geographic variation in minisatellite DNA was examined in 42 stocks of chum salmon, *Oncorhynchus keta*, from the eastern and western Pacific by restricting genomic DNA with *Hae*III and hybridizing it with two minisatellite probes. Regional differentiation in allelic frequencies at the two minisatellite loci was observed; Japanese stocks were distinct from Russian and Yukon River stocks, and stocks from those two regions were distinct from stocks in southeast Alaska and British Columbia. No significant annual variation was observed in allelic frequencies at the two loci for three stocks. Simulated mixed fishery samples of 100 Japanese chum salmon were resolved with a baseline of nine Japanese stocks with an average error of 0.5% per mixture stock. Similarly, simulated mixtures of Yukon River chum salmon resolved with a baseline of five stocks resulted in an average error of 0.6% per mixture stock. Fraser River chum salmon mixtures were resolved with an average error of 3% per mixture stock. With Asian and North American stocks pooled into two groups, accuracy of classification for individual fish to continent of origin was 78% for 323 Asian fish, and 94% for 797 North American fish. Minisatellite DNA variation can be successfully applied to problems of stock discrimination in chum salmon.

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Chum salmon, *Oncorhynchus keta*, have the widest natural geographic distribution of all Pacific salmon species, ranging in Asia from Korea to the Arctic coast of Russia, and in North America from California to the Arctic coast of Canada (Salo, 1991). Chum salmon support major fisheries in both Asia and North America, and management of the fisheries in North America usually requires that stock composition of the catches be determined in order to prevent excessive exploitation of particular stocks. A variety of methods have been applied to discriminate among chum salmon populations and to estimate stock composition in fisheries. Early work consisted in applying physical tags to individual fish (Pritchard, 1931; Anderson and Beacham, 1983), but quantitative estimates of stock composition were generally unable to be derived from these studies. Variation in scale characters has also been used for stock identification in chum salmon (Kovtun, 1983; Nikolayeva and Semenets, 1983; Ishida et al., 1989), but the ability to discriminate among stocks in a localized area is limited.

Genetic methods of stock identification for chum salmon have been evaluated by using both protein- and DNA-level variation. Stock identification techniques based upon genetic variation at protein-coding loci have been shown to provide information on stock structure (Okazaki, 1982; Omelchenko et al., 1992; Kondzela et al., 1994; Phelps et al., 1994; Winans et al., 1994) and stock composition in chum salmon fisheries (Beacham et al., 1985, 1987). By screening genetic variation at the DNA level, using mitochondrial DNA variation (Ginatulina and Mashkin, 1990; Ginatulina, 1992; Cronin et al., 1993; Park et al., 1993) and minisatellite DNA variation (Taylor et al., 1994), the population structure of a species can be determined. Variation in minisatellite DNA has been used to provide accurate and precise estimates of stock composition in simulated mixtures in a number of *Oncorhynchus* species (Beacham et al., 1995, 1996; Miller et al., 1996. Minisatellite DNA consists of tandemly repeated arrays of nucleotides where each array contains a core sequence (Jarman and Wells, 1989). Variable numbers of the tandem repeats (VNTR) occur between restriction sites, resulting in allelic variation at the minisatellite locus. Heterozygosity at these loci can be substantially greater than that commonly observed with protein electrophoresis. Average heterozygosity at protein electrophoretic loci is less than 10% in chum salmon (Winans et al., 1994); heterozygosities at minisatellite loci in salmonids are reported to be between 35 and 80% (Taggart and Ferguson, 1990; Bentzen and Wright, 1993; Taylor et al., 1996). The high level

of variation at minisatellite loci offers the potential for increased population differentiation in contrast with other methods of stock identification.

Initial screening of Asian and North American chum salmon populations with a single-locus minisatellite probe suggested that there were three regional groups of populations, namely Japanese, Russian and Yukon River, and southeast Alaska and British Columbia (Taylor et al., 1994). However, detection of population structure or differentiation among populations within the three major regional groups of chum salmon was limited, even though previous surveys of variation at protein-coding loci suggested that there was at least regional structuring within the British Columbia populations (Okazaki, 1982; Beacham et al., 1987). In the current study, variation at two additional minisatellite DNA loci is reported, and the efficacy of using variation at three minisatellite loci to discriminate among chum salmon populations in local areas is evaluated.

Materials and methods

Samples, laboratory procedures, and probes

The stocks surveyed, their geographic locations, and the methods of DNA extraction, restriction enzyme digestion (*Hae*III), Southern blotting, and membrane preparation have been outlined by Taylor et al. (1994). Summarized briefly, 4 µg of *Hae*III-digested DNA were loaded onto agarose gels containing 30 wells. For the 30 lanes on each gel, 4 lanes were used for λDNA restricted with *Hind*III and *Eco*RI as a molecular weight-size marker, and 26 lanes were used for genomic DNA, one of which was a control fish run. DNA was size-fractionated by electrophoresis in 0.8% agarose gels in 0.5× TBE buffer (45 mM Tris-borate, 1 mM EDTA, pH 8.0). After electrophoresis, the agarose gels were depurinated, alkali-denatured, and then the DNA was transferred under vacuum to nylon hybridization membranes and fixed to the membranes by crosslinking under ultraviolet illumination for 3 min.

The probes used in the laboratory analysis were p*Ssa*-A33 and p*Ssa*-A34, hypervariable minisatellite single locus probes in salmonids (Taggart and Ferguson, 1990; Prodöhl et al., 1994). Prior to hybridization with the target probe, the previous probe used was stripped from the membrane by the high temperature method outlined by Noppinger et al. (1992). Following hybridization with each probe, the membranes were washed twice in 2× SSC/0.1% SDS at room temperature for 15 min, once in 2× SSC/0.1% SDS at 65°C for 30 min, once in 1× SSC/0.1% SDS at 65°C for 30 min, and were given a final wash in 1× SSC at room temperature for 15 min. The probes were labelled with ^{32}P, and the membranes exposed to X-ray film. Up to 42 stocks of chum salmon were surveyed in the analysis (the term "stock" was used according to the sense of Ricker (1972), where a stock represents a discrete breeding unit spawning at a given time or place in a river).

Analysis of autoradiographs

The autoradiographs were analyzed with Bioimage software (Millipore Corp. Imaging Systems, Ann Arbor, MI) and scanned with a Kodak high-resolution two-dimensional charge coupled device (CCD) camera at a 1,024 × 1,024 pixel density. The images were translated into digital file images and stored at a workstation for later analysis. Lambda DNA-size markers (21.23, 5.15, 4.97, 4.27, 3.53, and 2.03 kilo base pairs [kbp]) were run on four lanes of each gel and used to create a size standard network that spanned the whole image. Molecular sizes were then assigned by the software to each fragment in each lane on the basis of their relationship to the size standard network. When the p*Ssa*-A33 and p*Ssa*-A34 probes were used, each lane contained either one or two bands; fish with a single band were considered homozygous and two comigrating bands of the same size were scored for those fish. The two probes detect alleles in chum salmon at a single locus where the alleles are inherited in a Mendelian fashion (unpublished data), as was observed for p*Ssa*-A34 in sockeye salmon, *O. nerka* (Taylor et al., 1996), and chinook salmon, *O. tshawytscha* (Stevens et al., 1993), and for both p*Ssa*-A33 and p*Ssa*-A34 in brown trout, *Salmo trutta* (Prodöhl et al., 1994).

Band assignment

Fish from one stock could be analyzed on multiple gels, and thus it was necessary to determine measurement error of band size among gels in order to combine the data. Precision of the estimation of band size was determined by analyzing a standard fish over all gels and by determining the relationship between precision of the estimate and fragment size as outlined by Taylor et al. (1994). As measurement error was present in the estimation of fragment size, a binning procedure (Gill et al., 1990; Galbraith et al., 1991) was used to assign each observed fragment to a particular size class or bin. Distribution of fragment sizes at the *Ssa*-A33 locus ranged from about 4 to 22 kbp, whereas the distribution at the *Ssa*-A34 locus ranged from 2.5 to 8.5 kbp, with very few fragments observed greater than 6.0 kbp (Fig. 1). Bin

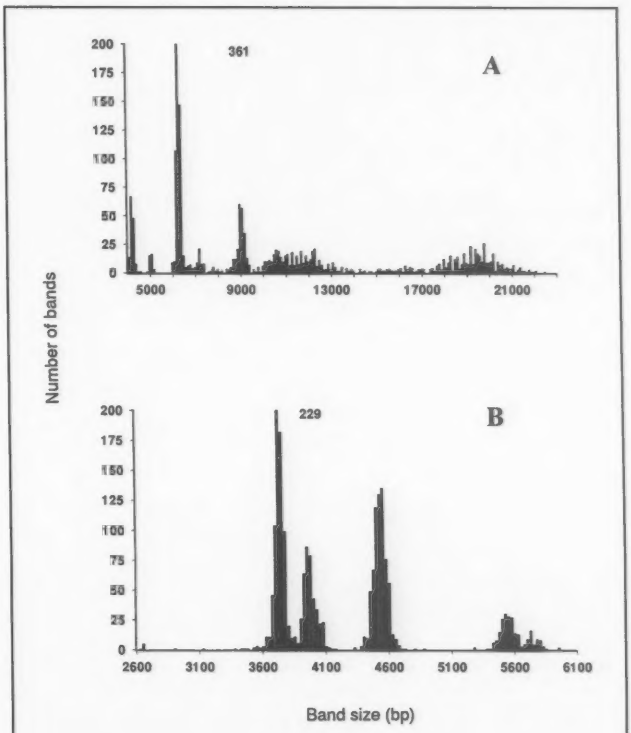

Figure 1

Observed frequency distribution of DNA band size over all chum salmon, *Oncorhynchus keta*, populations surveyed for variation with the probes p*Ssa*-A33 (**A**) and p*Ssa*-A34 (**B**). Frequencies of any band over 200 were truncated and the limits are indicated in the figure (i.e. 361 and 229).

intervals for definition of alleles at the *Ssa*-A33 locus were defined by 15 classes as outlined in Table 1, and bin intervals for definition of alleles at the *Ssa*-A34 locus were defined by 18 classes as outlined in Table 2. The average bin width was 9.8 standard deviations (SD) for bins containing bands <5,000 bp and 8.3 SD's for bins containing bands >5,000 bp. Variation previously observed with the *Ssa*1 probe was reanalyzed from the 44-bin characterization of Taylor et al. (1994) to a 31-bin characterization, with bin limits outlined by Beacham et al. (1996).

Data analysis

Mean allele frequencies were calculated by stock for *Ssa*-A33 and *Ssa*-A34 loci with the bins considered as alleles. Differences in heterozygosity among stocks in different areas were evaluated by the log-likelihood ratio or *G*-test statistic (Sokal and Rohlf, 1981). Annual variation in the allele frequency distributions was evaluated for each probe for three stocks that had been sampled over two years. The chi-square (χ^2) test with 1,000 Monte Carlo simulations of the distribution of the χ^2 statistic (Roff and Bentzen, 1989) was used to evaluate significance of annual variation in allele frequency distributions (McElroy et al., 1992). Genotype frequencies within populations were compared with those expected under Hardy-Weinberg equilibrium by 500 Monte Carlo simulations of the distribution of the χ^2 statistic. As the data set included both allele frequencies (*Ssa*-A33 and *Ssa*-A34) and band counts (*Ssa*1), a generalized or chord distance value (Pimentel, 1979) was calculated between each pair of stocks. A dendrogram was obtained by clustering the distance estimates by means of the neighbor-joining algorithm (Felsenstein, 1990). Classification of individual fish to specific stocks was conducted by using the DISCRIM procedure of SAS (SAS Institute Inc., 1989) with a jackknife sampling procedure, whereby classification

Table 1

Allele frequencies at the *Ssa*-A33 locus for 42 stocks of chum salmon. Genomic DNA was restricted with *Hae*III and hybridized with the p*Ssa*-A33 probe. Bin intervals for definition of alleles were: 4100–4400 bp (1), 4401–4700 bp (2), 4701–5000 bp (3), 5001–5500 bp (4), 5501–6000 bp (5), 6001–6500 bp (6), 6501–7000 bp (7), 7001–7700 bp (8), 7701–8500 bp (9), 8501–9300 bp (10), 9301–10,000 bp (11), 10,001–11,000 bp (12), 11,001–13,000 bp (13), 13,001–16,000 bp (14), >16,001 bp (15). *n* is sample size. North = two stocks from southeast Alaska and two from northern British Columbia; WCVI = west coast of Vancouver Island; ECVI = east coast of Vancouver Island; and Mainland = southern coastal mainland of British Columbia.

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Chitose	46	0.217	0.011	0.000	0.043	0.000	0.391	0.043	0.152	0.011	0.000	0.000	0.000	0.000	0.076	0.054
Tokachi	47	0.245	0.000	0.000	0.074	0.000	0.223	0.053	0.128	0.021	0.011	0.000	0.000	0.000	0.106	0.138
Miomoto	16	0.281	0.000	0.000	0.031	0.000	0.281	0.000	0.063	0.063	0.000	0.000	0.000	0.063	0.094	0.125
Ohkawa	8	0.188	0.063	0.000	0.125	0.000	0.250	0.000	0.063	0.000	0.063	0.000	0.000	0.063	0.125	0.063
Shibetsu	14	0.214	0.000	0.000	0.000	0.000	0.357	0.036	0.036	0.000	0.107	0.000	0.000	0.071	0.071	0.107
Teshio	8	0.250	0.000	0.000	0.063	0.000	0.313	0.000	0.000	0.188	0.000	0.000	0.000	0.125	0.063	0.000
Tokoro	10	0.350	0.000	0.000	0.000	0.000	0.150	0.050	0.300	0.000	0.000	0.000	0.000	0.000	0.050	0.100
Honoari	48	0.229	0.000	0.010	0.115	0.000	0.354	0.000	0.073	0.052	0.000	0.010	0.000	0.010	0.031	0.115
Abashiri	48	0.281	0.000	0.010	0.052	0.000	0.281	0.010	0.073	0.021	0.010	0.000	0.000	0.042	0.063	0.156
Total for Japan	245	0.247	0.004	0.004	0.063	0.000	0.304	0.024	0.102	0.031	0.012	0.002	0.000	0.024	0.071	0.110
Anadyr	34	0.147	0.000	0.000	0.000	0.000	0.485	0.000	0.000	0.000	0.088	0.029	0.000	0.103	0.029	0.118
Kanchalan	38	0.145	0.013	0.000	0.000	0.000	0.408	0.013	0.000	0.000	0.079	0.013	0.026	0.079	0.066	0.158
Ola	16	0.000	0.000	0.000	0.000	0.000	0.844	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.094
Kamchatka	9	0.111	0.000	0.000	0.000	0.000	0.389	0.000	0.000	0.000	0.056	0.056	0.056	0.000	0.167	0.167
Total for Russia	97	0.119	0.005	0.000	0.000	0.000	0.505	0.005	0.000	0.000	0.067	0.021	0.015	0.077	0.052	0.134
Andreafsky	35	0.043	0.000	0.000	0.000	0.000	0.529	0.000	0.043	0.000	0.000	0.014	0.000	0.014	0.000	0.358
Kluane	29	0.017	0.000	0.000	0.000	0.000	0.483	0.000	0.103	0.000	0.086	0.000	0.000	0.000	0.000	0.310
Fishing Branch	29	0.034	0.000	0.000	0.000	0.000	0.552	0.000	0.000	0.000	0.155	0.000	0.000	0.034	0.000	0.224
Sheenjek	28	0.071	0.000	0.000	0.000	0.000	0.589	0.018	0.000	0.000	0.214	0.000	0.000	0.000	0.000	0.107
Tatchun	28	0.000	0.000	0.000	0.000	0.000	0.714	0.018	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.143
Total for Yukon River	149	0.034	0.000	0.000	0.000	0.000	0.570	0.007	0.030	0.000	0.111	0.003	0.000	0.010	0.000	0.234
Fish Creek	46	0.000	0.000	0.000	0.000	0.000	0.402	0.120	0.000	0.000	0.033	0.000	0.011	0.087	0.000	0.347
Breezy Bay	42	0.000	0.000	0.000	0.000	0.000	0.405	0.012	0.000	0.000	0.048	0.012	0.012	0.036	0.000	0.476
Atnarko	24	0.000	0.000	0.000	0.000	0.000	0.583	0.000	0.000	0.000	0.000	0.000	0.042	0.042	0.000	0.333
Pallant	50	0.000	0.000	0.000	0.000	0.000	0.630	0.000	0.000	0.000	0.000	0.010	0.020	0.040	0.000	0.300
Total for North	162	0.000	0.000	0.000	0.000	0.000	0.500	0.037	0.000	0.000	0.022	0.006	0.019	0.052	0.000	0.364
Conuma	23	0.000	0.000	0.000	0.000	0.043	0.478	0.000	0.000	0.022	0.043	0.000	0.043	0.065	0.043	0.261
Nitinat	48	0.000	0.000	0.000	0.000	0.000	0.615	0.042	0.000	0.000	0.010	0.021	0.052	0.125	0.021	0.115
Demamiel	24	0.000	0.000	0.000	0.000	0.000	0.417	0.000	0.000	0.000	0.063	0.000	0.000	0.125	0.000	0.396
Total for WCVI	95	0.000	0.000	0.000	0.000	0.011	0.532	0.021	0.000	0.005	0.032	0.011	0.037	0.111	0.021	0.222

continued

Table 1 (continued)

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Alouette	23	0.000	0.000	0.000	0.000	0.000	0.283	0.000	0.000	0.000	0.087	0.000	0.130	0.196	0.022	0.282
Chehalis	24	0.000	0.000	0.000	0.000	0.000	0.354	0.021	0.000	0.000	0.042	0.000	0.063	0.250	0.000	0.271
Chilliwack	48	0.000	0.000	0.000	0.000	0.000	0.302	0.000	0.000	0.000	0.063	0.000	0.052	0.302	0.031	0.250
Inch	21	0.000	0.000	0.000	0.000	0.000	0.381	0.000	0.000	0.000	0.119	0.024	0.119	0.190	0.000	0.167
Stave	23	0.000	0.000	0.000	0.000	0.000	0.391	0.000	0.000	0.022	0.043	0.000	0.109	0.109	0.043	0.282
Wahleach	22	0.000	0.000	0.000	0.000	0.000	0.318	0.000	0.000	0.000	0.114	0.023	0.000	0.364	0.023	0.159
Total for Fraser River	161	0.000	0.000	0.000	0.000	0.000	0.332	0.003	0.000	0.003	0.075	0.006	0.075	0.245	0.022	0.240
Cowichan	22	0.000	0.000	0.000	0.000	0.000	0.159	0.000	0.000	0.000	0.023	0.000	0.045	0.386	0.000	0.387
Big Qualicum	59	0.000	0.000	0.000	0.000	0.000	0.246	0.008	0.000	0.000	0.051	0.000	0.085	0.237	0.042	0.331
Chemainus	24	0.000	0.000	0.000	0.000	0.000	0.229	0.000	0.000	0.000	0.167	0.000	0.125	0.208	0.000	0.271
Goldstream	24	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.104	0.000	0.021	0.333	0.021	0.188
L. Qualicum	36	0.000	0.000	0.000	0.014	0.000	0.194	0.014	0.056	0.000	0.056	0.042	0.028	0.153	0.139	0.306
Nanaimo	24	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.021	0.083	0.000	0.063	0.292	0.000	0.292
Puntledge	23	0.000	0.000	0.000	0.000	0.000	0.239	0.000	0.000	0.000	0.174	0.022	0.174	0.130	0.022	0.239
Total for ECVI	212	0.000	0.000	0.000	0.002	0.000	0.236	0.005	0.009	0.002	0.085	0.009	0.075	0.241	0.040	0.295
Tzoonie	23	0.000	0.000	0.000	0.000	0.000	0.239	0.000	0.000	0.000	0.043	0.022	0.043	0.283	0.065	0.304
Mamquam	28	0.000	0.000	0.000	0.018	0.000	0.214	0.000	0.000	0.000	0.125	0.018	0.018	0.304	0.071	0.232
Sliammon	6	0.000	0.000	0.000	0.000	0.000	0.500	0.083	0.000	0.000	0.167	0.000	0.083	0.083	0.000	0.083
Cheakamus	6	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.000	0.000	0.000	0.417	0.000	0.250
Total for Mainland	63	0.000	0.000	0.000	0.008	0.000	0.262	0.008	0.000	0.000	0.087	0.016	0.032	0.286	0.056	0.246

functions were developed with all fish sampled except the one to be classified. The accuracy of classification of individual fish was summarized both on a population and on a regional basis.

Estimation of stock composition

Baseline data

In this study, counts were available from 15 alleles at the *Ssa*-A33 locus, 18 alleles at the *Ssa*-A34 locus, and from 31 band counts at the *Ssa*1 locus for each fish. The maximum-likelihood model (Fournier et al., 1984) used in the estimation of stock composition requires that the characters used in the analysis be independent. When allele counts and band counts were used to characterize the chum salmon stocks, a principal-components analysis on the correlation matrix of the 64 variables in the study was conducted in order to obtain uncorrelated variables or principal components, as was described by Beacham et al. (1996). Summarized briefly, the PRINCOMP procedure in SAS was used in the principal-components analysis. The observed data (number of bands per bin) were standardized by subtracting the overall corresponding mean and by dividing by the corresponding bin standard deviation over all populations for the original variables. The original variables were then represented as factor scores for uncorrelated variables or principal components. The first 57 principal components accounted for 100% of the total observed variation. The input to the maximum-likelihood model required discrete frequency counts for each variable, and as outlined by Beacham et al. (1995), the continuous distributions of the principal component scores were represented as 12-bin histograms. Limits of the bins were as follows: ≤–2.50 (1), –2.49 to –1.50 (2), –1.49 to –1.00 (3), –0.99 to –0.60 (4), –0.59 to –0.30 (5), –0.29 to 0.00 (6), 0.00 to 0.29 (7), 0.30 to 0.59 (8), 0.60 to 0.99 (9), 1.00 to 1.49 (10), 1.50 to 2.49 (11), and ≥2.50 (12). Each stock was then characterized as an input matrix of 57 rows (principal components) and 12 columns (counts of principal component scores in each of the 12 bins).

Table 2

Allele frequencies at the *Ssa*-A34 locus for 42 stocks of chum salmon. Genomic DNA was restricted with *Hae*III and hybridized with the p*Ssa*-A34 probe. Bin intervals for definitions of alleles were as follows: 2600–2700 bp (1), 2701–2800 bp (2), 2801–2900 bp (3), 2901–3100 bp (4), 3101–3300 (5), 3301–3500 bp (6), 3501–3700 bp (7), 3701–3900 bp (8), 3901–4100 bp (9), 4101–4400 bp (10), 4401–4700 bp (11), 4701–5000 bp (12), 5001–5500 bp (13), 5501–6000 bp (14), 6001–6500 bp (15), 6501–7000 bp (16), 7001–7700 bp (17), 7701–8500 bp (18). *n* is sample size. Abbreviations for geographic regions are defined in Table 1.

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Chitose	46	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.054	0.446	0.022	0.152	0.000	0.022	0.250	0.000	0.000	0.000	0.043
Tokachi	48	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.104	0.302	0.021	0.240	0.010	0.010	0.250	0.000	0.010	0.021	0.000
Miomoto	16	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.094	0.563	0.000	0.125	0.000	0.031	0.156	0.000	0.000	0.000	0.000
Ohkawa	16	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.656	0.000	0.094	0.000	0.000	0.219	0.000	0.031	0.000	0.000
Shibetsu	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.321	0.000	0.357	0.000	0.071	0.214	0.000	0.000	0.000	0.000
Teshio	8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.188	0.375	0.000	0.188	0.000	0.063	0.188	0.000	0.000	0.000	0.000
Tokoro	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.350	0.000	0.250	0.000	0.100	0.250	0.000	0.000	0.000	0.000
Honoari	48	0.000	0.000	0.000	0.000	0.000	0.010	0.031	0.115	0.344	0.000	0.240	0.010	0.094	0.156	0.000	0.000	0.000	0.000
Abashiri	48	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.083	0.375	0.000	0.240	0.000	0.042	0.219	0.010	0.000	0.000	0.000
Total for Japan	254	0.000	0.000	0.000	0.000	0.000	0.004	0.020	0.083	0.394	0.008	0.213	0.004	0.043	0.215	0.002	0.004	0.004	0.008
Anadyr	25	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.100	0.060	0.040	0.640	0.000	0.000	0.120	0.000	0.000	0.000	0.000
Kanchalan	39	0.000	0.000	0.000	0.000	0.013	0.013	0.013	0.282	0.064	0.000	0.590	0.000	0.000	0.026	0.000	0.000	0.000	0.000
Ola	15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.200	0.067	0.000	0.600	0.000	0.000	0.100	0.000	0.033	0.000	0.000
Kamchatka	13	0.000	0.000	0.000	0.000	0.000	0.000	0.038	0.269	0.038	0.000	0.538	0.000	0.000	0.115	0.000	0.000	0.000	0.000
Total for Russia	92	0.000	0.000	0.000	0.000	0.005	0.005	0.022	0.217	0.060	0.011	0.598	0.000	0.000	0.076	0.000	0.005	0.000	0.000
Andreafsky	36	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.236	0.069	0.000	0.611	0.000	0.000	0.069	0.000	0.000	0.000	0.000
Kluane	30	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.217	0.300	0.017	0.467	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fishing Br	29	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.224	0.241	0.000	0.448	0.000	0.000	0.086	0.000	0.000	0.000	0.000
Sheenjek	28	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.286	0.125	0.000	0.571	0.000	0.000	0.018	0.000	0.000	0.000	0.000
Tatchun	28	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.268	0.286	0.000	0.393	0.000	0.000	0.054	0.000	0.000	0.000	0.000
Total for Yukon River	151	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.245	0.199	0.003	0.503	0.000	0.000	0.046	0.000	0.000	0.000	0.000
Fish Creek	48	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.563	0.125	0.000	0.271	0.010	0.000	0.031	0.000	0.000	0.000	0.000
Breezy Bay	46	0.000	0.000	0.000	0.000	0.000	0.011	0.054	0.413	0.098	0.000	0.348	0.000	0.011	0.065	0.000	0.000	0.000	0.000
Atnarko	24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.396	0.083	0.000	0.417	0.000	0.000	0.104	0.000	0.000	0.000	0.000
Pallant	50	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.510	0.110	0.000	0.260	0.010	0.000	0.110	0.000	0.000	0.000	0.000
Total for North	168	0.000	0.000	0.000	0.000	0.000	0.003	0.015	0.482	0.107	0.000	0.310	0.006	0.003	0.074	0.000	0.000	0.000	0.000
Conuma	23	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.522	0.130	0.000	0.304	0.000	0.000	0.022	0.000	0.000	0.000	0.000
Demamiel	23	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.391	0.174	0.000	0.370	0.000	0.022	0.043	0.000	0.000	0.000	0.000
Nitinat	48	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.354	0.115	0.000	0.417	0.000	0.010	0.063	0.000	0.000	0.000	0.000
Total for WCVI	94	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.404	0.133	0.000	0.378	0.000	0.011	0.048	0.000	0.000	0.000	0.000

continued

Table 2 (continued)

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Alouette	23	0.000	0.000	0.000	0.000	0.000	0.000	0.152	0.348	0.130	0.065	0.130	0.000	0.043	0.130	0.000	0.000	0.000	0.000
Chehalis	24	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.333	0.208	0.000	0.354	0.000	0.021	0.021	0.000	0.000	0.000	0.000
Chilliwack	48	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.417	0.208	0.000	0.281	0.000	0.010	0.073	0.000	0.000	0.000	0.000
Inch	21	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.381	0.095	0.000	0.381	0.000	0.000	0.095	0.000	0.000	0.000	0.000
Stave	23	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.543	0.174	0.022	0.130	0.022	0.000	0.065	0.000	0.000	0.000	0.000
Wahleach	22	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.477	0.068	0.000	0.318	0.000	0.000	0.068	0.000	0.000	0.000	0.000
Total for Fraser River	161	0.006	0.000	0.000	0.000	0.000	0.000	0.050	0.416	0.158	0.012	0.267	0.003	0.012	0.075	0.000	0.000	0.000	0.000
Cowichan	22	0.023	0.000	0.000	0.000	0.000	0.000	0.045	0.591	0.045	0.000	0.250	0.000	0.000	0.045	0.000	0.000	0.000	0.000
Big Qualicum	58	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.612	0.121	0.017	0.181	0.000	0.000	0.043	0.000	0.009	0.000	0.000
Chemainus	24	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.458	0.229	0.000	0.208	0.000	0.021	0.042	0.000	0.000	0.000	0.000
Goldstream	23	0.000	0.000	0.000	0.000	0.000	0.000	0.065	0.457	0.196	0.022	0.217	0.000	0.000	0.043	0.000	0.000	0.000	0.000
L. Qualicum	36	0.000	0.000	0.000	0.014	0.000	0.000	0.028	0.625	0.069	0.014	0.236	0.000	0.014	0.014	0.000	0.000	0.000	0.000
Nanaimo	24	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.417	0.146	0.000	0.292	0.000	0.021	0.042	0.000	0.000	0.000	0.000
Puntledge	23	0.000	0.000	0.000	0.000	0.000	0.000	0.152	0.261	0.043	0.000	0.413	0.000	0.065	0.065	0.000	0.000	0.000	0.000
Total for ECVI	210	0.007	0.000	0.000	0.002	0.000	0.000	0.048	0.517	0.119	0.010	0.243	0.000	0.014	0.040	0.000	0.002	0.000	0.000
Tzoonie	24	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.479	0.167	0.000	0.208	0.000	0.000	0.083	0.000	0.042	0.000	0.000
Mamquam	29	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.397	0.172	0.017	0.345	0.000	0.000	0.052	0.000	0.000	0.000	0.000
Sliammon	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.692	0.077	0.000	0.192	0.000	0.000	0.038	0.000	0.000	0.000	0.000
Cheakamus	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.462	0.115	0.000	0.346	0.000	0.000	0.077	0.000	0.000	0.000	0.000
Total for Mainland	79	0.006	0.000	0.000	0.000	0.000	0.000	0.006	0.481	0.146	0.006	0.278	0.000	0.000	0.063	0.000	0.013	0.000	0.000

Mixture data

A series of hypothetical fishery samples that contained fish from a specific region or stock were analyzed in order to evaluate the use of minisatellite DNA for stock composition. Test samples of 100 fish were generated 50 times by randomly resampling with replacement stocks from the appropriate river or region; then the mean and standard deviation of the 50 estimates were computed. Stock compositions of the mixture were determined under the assumption that the baseline data were perfectly representative of the stocks (fixed-frequency distribution) and by simulating random variation involved in the collection of baseline samples (resampled distribution). Each baseline stock was resampled with replacement to obtain new distributions of the principal components with the same sample size as in the original sample (Millar, 1990).

Results

Geographic variation in *Ssa*-A33 allele frequencies

Allele size varied from 4.1 to 21.3 kbp (Fig. 2). Major alleles were observed at the 4.1 to 4.4 kbp (bin 1), 6.0 to 6.5 kbp (bin 6), and 8.5 to 9.3 kbp (bin 10) (Fig. 1; Table 1). Variation in allele frequencies was observed among Japanese, Russian, and Yukon rivers, and other North American stocks. An allele between 4.1 and 4.4 kbp was fairly common in Japanese stocks (mean frequency 0.25), less common in Russian stocks (0.12), and absent in North American stocks south of the Yukon River (Table 1). Similarly, alleles greater than 16.0 kbp were fairly rare in Asian stocks (Japanese stock mean frequency: 0.11; Russian: 0.13) but were more common in North American stocks (regional frequencies: 0.24–0.26). Clear differences in allele frequencies were observed in chum salmon stocks in broadly separated geographic areas.

In North American stocks, regional differences in allelic frequencies were observed. Mean frequency of the 11.0–13.0 kbp allele was 0.01 for Yukon River stocks, 0.05 for southeast Alaska and northern British Columbia stocks, 0.11 for west coast of Vancouver Island (WCVI) stocks, and 0.24

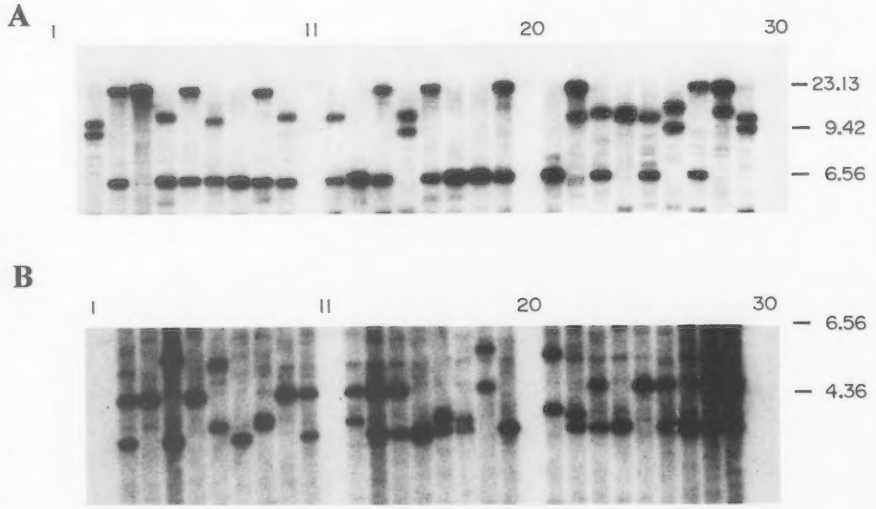

Figure 2

Autoradiographs of chum salmon DNA restricted with *Hae*III and hybridized with the probe p*Ssa*-A33 (**A**) or p*Ssa*-A34 (**B**). In panel A, lanes 1, 11, 20, and 30 represent size-standard fish; lanes 2 and 29 represent standard fish; lanes 3–8, 16–19, and 21–22 represent Atnarko fish; and 9–10, 12–15, and 23–28 represent Chilliwack fish. In panel B, the lanes are similar; Chilliwack chum salmon DNA is seen in lanes 3–8, 16–19, and 21–22, and Nitinat chum salmon DNA in lanes 9–10, 12–15, and 24–29.

or greater for east coast of Vancouver Island (ECVI), mainland British Columbia, or Fraser River stocks (Table 1). However, within a region, marked differences in allelic frequencies could be observed among stocks. For example, frequency of the allele greater than 16.0 kbp ranged between 0.16 and 0.28 for six Fraser River stocks, and frequency of the 11.0–13.0 kbp allele ranged between 0.13 and 0.39 for seven ECVI stocks. This variation in allele frequencies among stocks within regions may allow discrimination among stocks within the region but it increases the complexity of discriminating among stocks between regions.

Genotypic frequencies at the *Ssa*-A33 locus were in Hardy-Weinberg equilibrium in all 42 stocks sampled. On a regional basis, heterozygosity ranged from 54 to 72% for the stocks sampled, with Japanese stocks significantly more heterozygous than the pooled aggregate of North American stocks (G=6.03, df=1, P<0.05)(Table 1).

Geographic variation in *Ssa*-A34 allele frequencies

Allele size varied from 2.6 to 8.5 kbp (Fig. 2), with major alleles at 3.7–3.9 kbp (bin 8), 3.9–4.1 kbp (bin 9), and 4.4–4.7 kbp (bin 11) (Fig. 1; Table 2). As with the *Ssa*-A33 locus, differences in allele frequencies were observed among Japanese, Russian, and North American stocks. Of the Russian stocks surveyed, all had a relatively high frequency (mean 0.60) of the 4.4–4.7 kbp allele, significantly different from Japanese stocks (mean 0.21)(χ^2=89.6, df=1, P<0.01)(Table 2). Mean frequency of the 3.7–3.9 kbp allele was 0.08 in Japanese stocks, 0.22–0.25 in Russian and Yukon River stocks, and 0.40–0.52 in southeast Alaska and British Columbia stocks. Similar patterns of the genetic distinctiveness of the major stock groups were observed at both the *Ssa*-A33 and *Ssa*-A34 loci.

In British Columbia, regional differences in allele frequencies were fairly minor in comparison with the variation among stocks within regions (Table 2). For example, in the six Fraser River stocks, frequencies of the 4.4–4.7 kbp allele ranged from 0.13 to 0.38 (mean 0.27), in the seven ECVI stocks from 0.18 to 0.41 (mean 0.24), and in the four mainland stocks from 0.19 to 0.35 (mean 0.28). The variation in allele frequencies among stocks within regions may be used effectively for localized stock discrimination, but as with the *Ssa*-A33 locus, makes discrimination among regional groups of stocks more difficult.

Table 3

Observed heterozygosities for chum salmon, *Oncorhyncus keta*, from eight regions at the *Ssa*-A33 and *Ssa*-A34 loci. Stocks sampled within each region are listed in Tables 1 and 2. *n* = number of fish sampled in each region. Stocks sampled in each region are outlined in Table 1. Abbreviations for geographic regions are defined in Table 1.

Region	*n*	*Ssa*-A33	*n*	*Ssa*-A34
Japan	245	0.718	254	0.768
Russia	97	0.629	92	0.620
Yukon	149	0.557	151	0.642
North	162	0.568	168	0.655
WCVI	95	0.537	94	0.713
Fraser	161	0.720	161	0.658
ECVI	212	0.703	210	0.579
Mainland	63	0.651	79	0.633

As with the *Ssa*-A33 locus, genotypic frequencies at the *Ssa*-A34 locus were in Hardy-Weinberg equilibrium in all of the 42 stocks sampled. Mean heterozygosity of the Japanese stocks (0.77) was higher than that for any other regional group of stocks (Table 3) and significantly higher than that for North American (G=15.0, df=1, P<0.05) or Russian stocks (G=6.50, df=1, P<0.05). Heterozygosity of Japanese chum salmon was consistently higher than that for other regional groups of chum salmon when both the *Ssa*-A33 and *Ssa*-A34 loci were considered.

Annual variation in allele frequencies

Samples from two Vancouver Island (Big Qualicum, Nitinat) stocks and one Fraser River (Chilliwack) stock were obtained in both 1991 and 1992. No significant annual variation was observed in allele frequencies at either the *Ssa*-A33 or *Ssa*-A34 loci for any stock (P>0.05)(6 tests conducted).

Stock structure

Neighbor-joining analysis of the distances between stocks derived from allele frequencies at the *Ssa*-A33 and *Ssa*-A34 loci and from band counts observed with the *Ssa*1 probe indicated that Japanese chum salmon stocks were distinct from all other groups of stocks (Fig. 3). Regional stock structure was also examined with principal-components analysis, and all nine Japanese stocks sampled were clearly separated from all other stocks (Fig. 4). Russian and Yukon River stocks were more similar to each other than to more distant stocks in Japan and British Columbia (Figs. 3 and 4). There was weak regional structuring among stocks of British Columbia chum salmon, and there was some evidence that southeast Alaska and northern British Columbia stocks were more similar to each other than to stocks in southern British Columbia (Fig. 3) and some evidence that there was separation between ECVI and Fraser River stocks (Fig. 4).

Estimation of stock composition

The potential use of minisatellite DNA variation for estimation of stock composition of stocks from broad geographic areas was evaluated for two main groupings of chum salmon, namely mixtures of Japanese and Russian chum salmon and mixtures of Russian and Yukon River chum salmon. On the basis of stock structure, relatively accurate and precise estimates of stock composition should be derived from samples containing Japanese and Russian chum salmon (Table 4). Similarly, in applications where estimation of Russian and Yukon River chum salmon compositions is of interest, relatively accurate and precise estimates of stock composition of the two target groups should be derived (Table 4). The Andrefsky River stock was in a group with Russian stocks in the neighbor-joining analysis (Fig. 3) but seemed separable from Russian stocks in the principal-components analysis (Fig. 4). The simulations suggested that even if the Andrefsky River comprised all the Yukon River component, separation of Russian and Yukon River stock components should still be possible (Table 4).

The application of minisatellite DNA variation to local stock composition issues was evaluated for three situations; i.e. mixtures of Japanese, Yukon River, and southern British Columbia chum salmon stocks were evaluated separately. The simulations suggested that both discrimination among all of the Japanese stocks sampled and relatively accurate estimates of stock composition observed in both single-stock and multistock simulated mixtures were possible (Table 5). Because less than 20 fish per stock were sampled for five of the nine stocks surveyed (Table 1), increased baseline sampling, however, would be required to confirm these results before application to actual fishery samples. The simulations of Yukon River chum salmon mixtures suggested that all five stocks were distinct from each other and that accurate estimates of stock composition may be possible with minisatellite DNA variation (Table 6). The fall-run Sheenjek River stock was distinguishable from fall-run stocks spawning in the Yukon Territory. The simulations of southern British Columbia chum salmon mixtures suggested that minisatellite DNA variation may be applicable for estimation of stock composition in fishery samples. Estimates of stock composition for

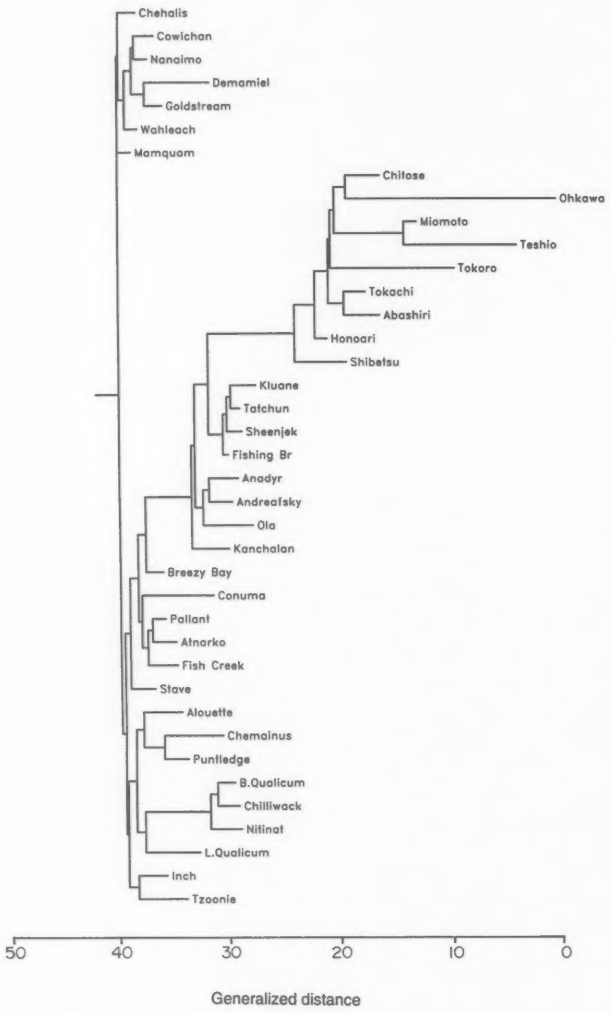

Figure 3

A neighbor-joining dendrogram of relationships among 39 stocks of chum salmon based on allele frequencies at the *Ssa*-A33 and *Ssa*-A34 loci and on band counts of occurrence for the probe *Ssa*1.

the six individual Fraser River stocks, derived from a baseline for Fraser River only, indicate that discrimination among the stocks was possible (Table 7). Similar results were also observed when an ECVI-only or WCVI-only baseline was used and when ECVI and WCVI fish were in the simulated mixtures as appropriate. When an 18-stock regional baseline was used, there was a clear indication of separation among Fraser River, ECVI, and WCVI stocks (Table 7).

Identification of individuals

The accuracy of classifying individuals to specific stocks or regions was dependent upon the specific stock under consideration; the greatest accuracy was observed for the more distinctive stocks or regional groups. With a 39-stock baseline (Sliammon, Cheakamus, and Kamchatka were removed owing to lack of *Ssa*1 band counts), classification accuracy

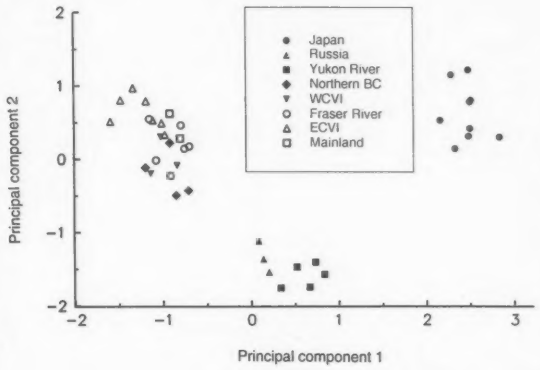

Figure 4

Plot of first two principal components (PC) incorporating variation at the *Ssa*-A33 and *Ssa*-A34 loci and including *Ssa*-1 band counts for 39 stocks indicated in Figure 2. North = two stocks from southeast Alaska and two stocks from northern British Columbia. WCVI = west coast of Vancouver Island; ECVI = east coast of Vancouver Island; Mainland = southern coastal mainland of British Columbia.

for Japanese chum salmon to specific stocks averaged 15%, but 82% were correctly identified as Japanese in origin (Table 8). Similarly, classification accuracy for Russian chum salmon to stock of origin was 30%, and to region of origin, 47%. Yukon River chum salmon were fairly distinctive and the origin of about 75% of the fish was correctly identified. Accurate classification for individual southern British Columbia chum salmon to region of origin ranged from about 9 to 44% (Table 8), presumably reflecting less separation among these groups compared with that among Japanese, Russian, and Yukon River chum salmon. With Asian and North American stocks pooled into two groups, accuracate classification to continent of origin for 323 Asian fish was 78%, and that for 797 North American fish was 94%. The minisatellite DNA variation provided a reasonable measure of accuracy in classifying individuals to continent of origin.

Discussion

Allele frequencies at the *Ssa*-A33 and *Ssa*-A34 loci indicated that there were three regional groups of chum salmon stocks: the Japanese, Russian and Yukon River, and southeast Alaska and British Columbia stocks. The greatest differences were observed between stocks from Japan and British Columbia. Similar results were also observed in a survey of minisatellite DNA variation with the *Ssa*1 probe (Taylor et al., 1994). The differentiation between stocks from Japan and British Columbia has also been demonstrated in studies of variation at protein-coding loci (Okazaki, 1982) and more recently in mitochondrial DNA in the region coding for NADH dehydrogenase subunits 5 and 6 (Park et al., 1993). These results are consistent with the conclusion that stocks that are more distant geographically also show more distinct genetic differentiation (Taylor et al., 1994). These patterns presumably reflect the dispersal of salmon from different refuges after the retreat of glaciers at the end of the Wisconsinian glacial period (Lindsey and McPhail, 1986). The separation between Japanese and Russian stocks reported by Winans et al. (1994) in a survey of variation at protein-coding loci was also observed in the current study with variation at minisatellite loci. A high degree of genetic differentiation has been consistently observed between Japanese and North American chum salmon, regardless of

Table 4

Estimated percentage composition of a variety of mixtures of chum salmon. Each mixture of 100 fish was generated 50 times with replacement, and a stock composition of the mixtures estimated by using either a fixed distribution of the allele frequencies or band counts in the baseline stocks, or by randomly resampling each baseline stock with replacement to obtain a resampled distribution of the frequencies or counts for each baseline stocks, with the same sample size in the new distribution as in the original one. Band frequencies used included those derived from genomic DNA restricted with *Hae*III and hybridized with *Ssa*-1, p*Ssa*-A33, and p*Ssa*-A34. Twelve (9 Japanese, 3 Russian) baseline stocks were used to resolve the Japanese and Russian mixtures, and 8 (3 Russian, 5 Yukon) baseline stocks for Russian and Yukon River chum salmon mixtures. Standard deviations are given in parentheses.

		Distribution (%)	
Origin	Actual	Fixed	Resampled
Japan vs. Russia			
Japan	0	0.0 (0.0)	5.2 (4.2)
Japan	25	24.8 (0.4)	28.3 (4.3)
Japan	50	49.5 (0.6)	51.3 (5.4)
Japan	75	74.7 (0.05)	74.5 (4.8)
Japan	100	99.6 (0.6)	99.6 (0.9)
Russia vs.Yukon			
Russia	0	0.1 (0.4)	3.6 (3.5)
Russia	25	24.1 (1.4)	28.2 (3.6)
Russia	50	48.3 (1.5)	49.9 (4.7)
Russia	75	72.4 (1.9)	72.5 (3.9)
Russia	100	97.5 (1.8)	96.0 (3.7)
Andreafsky	100	100.0 (0.0)	94.5 (5.0)

Table 5

Estimated percentage composition of 100-fish mixtures of Japanese chum salmon stocks resolved with a 9-stock baseline in which distributions of the allele frequencies or band counts in each baseline stock were fixed or resampled as outlined in Table 4. Standard deviations are given in parentheses.

		Distribution (%)	
Stock	Actual	Fixed	Resampled
Single-stock mixtures			
Chitose	100	100.0 (0.0)	94.1 (4.5)
Tokachi	100	100.0 (0.0)	94.4 (5.2)
Miomoto	100	100.0 (0.0)	91.0 (9.6)
Ohkawa	100	100.0 (0.0)	91.8 (10.4)
Shibetsu	100	100.0 (0.0)	92.3 (7.8)
Teshio	100	100.0 (0.0)	87.6 (13.5)
Tokoro	100	100.0 (0.0)	97.2 (5.8)
Honoari	100	100.0 (0.0)	94.2 (4.8)
Abashiri	100	100.0 (0.0)	93.2 (5.2)
Multistock mixture			
Chitose	10	9.7 (0.5)	11.0 (4.1)
Okachi	20	20.3 (0.6)	19.4 (3.0)
Honoari	30	30.2 (0.3)	29.7 (4.4)
Abashiri	40	39.8 (0.6)	39.8 (4.5)

Table 6

Estimated percentage composition of 100-fish mixtures of Yukon River chum salmon stocks resolved with a 5-stock baseline in which distributions of the allele frequencies or band counts in the baseline stock were fixed or resampled as outlined in Table 4. Standard deviations are given in parentheses.

		Distribution (%)	
Stock	Actual	Fixed	Resampled
Single-stock mixtures			
Andreafsky	100	100.0 (0.0)	97.0 (3.3)
Sheenjek	100	98.2 (1.7)	97.5 (3.1)
Fishing Branch	100	96.5 (2.0)	95.1 (4.1)
Tatchun	100	100.0 (0.0)	98.7 (3.4)
Kluane	100	100.0 (0.0)	95.9 (4.6)
Multistock mixture			
Kluane	10	9.3 (0.8)	10.0 (2.4)
Tatchun	20	20.3 (0.7)	19.8 (3.7)
Sheenjek	30	30.3 (0.4)	30.8 (4.0)
Fishing Branch	40	39.1 (1.1)	38.8 (4.5)

whether the survey has used protein electrophoretic, mitochondrial DNA, or minisatellite DNA variation.

In the current study, DNA bands were grouped in bins or "alleles" on the basis of the estimated size of the DNA fragment. The precision of estimated fragment size was based on analyzing a single standard fish on all gels, on obtaining repeated estimates of fragment size, and on determining a relationship between estimated fragment size and precision or standard deviation of the estimate (Galbraith et al., 1991; Taylor et al., 1994). The bin width was set at 8 to 10 SD, less than the 16 SD suggested by Galbraith et al. (1991) as necessary before the chances of assigning a band to the wrong bin falls below 0.05. However, because most of the source of variation in the Galbraith et al. (1991) study was due to digitizing bands that were manually marked on an acetate overlay, the computerized estimation system employed in the present study should result in greater precision of estimation of fragment size. Taylor et al. (1994) used a bin width of 6 SD, based upon the measurement precision of the fragment size of a standard fish, but a more conservative bin width of 8 to 10 SD was used in the current study.

The variation observed at the minisatellite loci examined in the current study was probably less than that actually present at the loci. Given the level of precision of the measurements of fragment size, closely spaced true alleles could not be distinguished reliably and were therefore combined in the binning process. It was assumed that there was no consistent bias in the assignment of fragments to specific bins. Additionally, differences in DNA sequence variation of two alleles of the same size were not determined. It is possible, for example, that an allele occurring in both Japanese and North American populations will show the same length for both populations but will reveal a considerably different DNA sequence.

The simulations conducted for mixtures containing localized stocks (Japan, Yukon River, and Fraser River) suggested that the minisatellite DNA variation surveyed may provide relatively accurate and precise estimates of individual stocks in the mixtures. Although the simulations were encouraging, the performance of the minisatellite DNA variation for estimation of stock composition needs to be verified by actual applications in field situations, where fish in the mixture can originate from stocks not found in the baseline, and where novel genotypes can be observed. In the present study, sample sizes of the baseline stocks were usually less than 50 fish; therefore, increased sampling of individuals in the stocks would be required in order to obtain representative distributions of allele frequencies or band counts.

The simulations suggested that accurate estimates of stock composition of individual stocks may be possible for mixtures of either Fraser River or Yukon River chum salmon. A previous survey of variation at seven protein-coding loci indicated that there was

Table 7

Estimated percentage composition of 100-fish mixtures of southern British Columbia chum salmon resolved with either an area-specific baseline (Fraser: 6 stocks; ECVI: 7 stocks; WCVI: 3 stocks) or an 18-stock baseline of southern stocks in which distributions of the allele frequencies or band counts in the baseline stocks were fixed or resampled as outlined in Table 4. The area sum is the total percentage allocated to all area stocks when the 18-stock regional baseline was used to resolve the mixtures. Standard deviation are given in parentheses. Abbreviations for geographic regions are defined in Table 1.

		Fixed			Resampled		
	Actual	Area baseline	Regional baseline	Area sum	Area baseline	Regional baseline	Area sum
Fraser River							
Single-stock mixtures							
Wahleach	100	95.5 (2.4)	95.5 (2.0)	100.0 (0.0)	93.9 (6.3)	87.1 (9.3)	93.1 (7.3)
Alouette	100	95.5 (2.4)	95.5 (2.4)	100.0 (0.0)	96.6 (3.6)	87.7 (7.9)	91.2 (7.9)
Chehalis	100	95.0 (2.9)	95.6 (2.0)	100.0 (0.0)	91.3 (6.7)	82.3 (8.6)	87.9 (8.6)
Chilliwack	100	100.0 (0.0)	100.0 (0.0)	100.0 (0.0)	98.4 (3.1)	85.4 (7.6)	87.4 (6.4)
Inch	100	100.0 (0.0)	100.0 (0.0)	100.0 (0.0)	95.1 (6.2)	93.0 (9.3)	93.8 (8.3)
Stave	100	92.0 (2.3)	92.0 (2.6)	100.0 (0.0)	88.6 (6.2)	82.2 (9.9)	91.8 (8.4)
Multi-stock mixture							
Wahleach	10	9.5 (0.7)	9.7 (0.5)	100.0 (0.0)	10.0 (2.6)	9.0 (2.8)	88.8 (5.1)
Alouette	20	19.1 (0.9)	18.9 (0.8)		17.5 (3.4)	16.0 (2.8)	
Chehalis	30	27.7 (1.4)	27.6 (1.3)		26.9 (4.7)	23.7 (3.9)	
Chilliwack	40	43.7 (1.8)	43.7 (1.6)		45.3 (4.8)	39.3 (5.3)	
ECVI							
Multi-stock mixture							
Cowichan	10	10.0 (0.0)	9.5 (0.6)	94.0 (2.8)	9.1 (2.1)	8.7 (2.1)	92.8 (3.8)
Nanaimo	20	20.0 (0.0)	18.8 (1.1)		18.2 (3.4)	16.4 (3.8)	
Little Qualicum	30	29.3 (0.7)	28.9 (0.8)		26.2 (3.6)	26.6 (4.2)	
Big Qualicum	40	40.7 (0.7)	36.8 (2.1)		46.3 (4.8)	42.0 (5.5)	
WCVI							
Multi-stock mixture							
Demamiel	20	20.0 (0.0)	19.3 (0.9)	98.2 (1.2)	18.4 (3.2)	17.0 (3.6)	89.0 (5.0)
Conuma	30	30.0 (0.0)	30.0 (0.0)		27.5 (4.3)	24.5 (3.2)	
Nitinat	50	50.0 (0.0)	48.9 (0.9)		54.1 (5.1)	47.6 (5.4)	

no marked distinction among Fraser River stocks (Beacham et al., 1987). Minisatellite DNA variation may provide the means to discriminate among Fraser River stocks if necessary in management applications. In the Yukon River drainage, summer-run stocks were well differentiated from fall-run stocks by analysis of variation at protein-coding loci (Wilmot et al., 1992, 1994). However, in the fall-run stocks, which spawn in rivers in both Alaska and the Yukon Territory, some stocks spawning in Alaskan rivers (Sheenjek and Chandalar rivers) were more similar to stocks spawning in the Yukon Territory rivers in Canada than they were to other Alaskan fall-run stocks. The addition of minisatellite DNA variation to techniques of stock discrimination may provide more accurate estimates of stock composition in mixed stocks (e.g. Canadian and American stocks).

Compared with some other methods of stock identification that are based upon biological tags, genetic-based methods of stock identication generally have the advantage of temporal stability of the characters used. For example, variation at protein-coding loci has usually been found to be temporally stable (Beacham et al., 1985, 1987; Kondzela et al., 1994; Wilmot et al., 1994), and similar results have been reported for minisatellite loci (Taylor et al., 1994; Beacham et al., 1996). The two-year temporal stability of allelic frequencies at the *Ssa*-A33 and *Ssa*-A34 loci observed in the current study suggests that annual sampling of contributing baseline stocks would not be required in order to estimate stock composition of appropriate mixtures. Because the populations sampled in this study tended to be major ones (escapement of British Columbia populations is usually >10,000 fish), the ratio of sample size to effective population size was less than 0.1, and the probability of a significant test to detect temporal variation is similar to the presumed level of significance (Waples, 1989).

Table 8

Percentage of correct classification of individual fish with discriminant analyses for 39 stocks of chum salmon. The percentage of fish that were correctly classified to stock is indicated, as is the percentage of fish classified to other stocks in the same and other regions. Results listed are for jackknife samples, in which the fish tested were not included in the sample used to derive the discriminant functions. The regional percentage correct is the sum of the percentage of fish correctly classified to stock and the percentage classified to other stocks within the same region. n = the number of fish classified in each stock. Abbreviations for geographic regions are defined in Table 1.

Stock	n	Correct	Japan	Russia	Yukon	North	ECVI	WCVI	Fraser	Mainland	Regional
Chitose	46	19.6	58.7	2.2	6.5	6.5	0.0	0.0	4.3	2.2	78.3
Tokachi	47	10.6	76.7	2.1	2.1	2.1	2.1	0.0	2.1	2.1	87.3
Miomoto	16	0.0	87.5	6.3	6.3	0.0	0.0	0.0	0.0	0.0	87.5
Ohkawa	8	0.0	62.5	0.0	25.0	0.0	0.0	0.0	0.0	12.5	62.5
Shibetsu	14	14.3	50.0	0.0	21.4	7.1	7.1	0.0	0.0	0.0	64.3
Teshio	8	37.5	50.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	87.5
Tokoro	10	30.0	60.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	90.0
Honoari	48	14.6	66.7	0.0	4.2	4.2	4.2	0.0	6.2	0.0	81.3
Abashiri	47	17.0	66.0	4.2	6.4	2.1	2.1	0.0	2.1	0.0	83.0
Japan	244	15.2	66.4	2.0	6.6	3.3	2.0	0.0	2.8	1.6	81.6
Anadyr	25	40.0	0.0	12.0	20.0	12.0	0.0	0.0	16.0	0.0	52.0
Kanchalan	39	25.6	5.1	18.0	25.6	7.7	10.2	0.0	7.7	0.0	43.6
Ola	15	26.7	20.0	20.0	20.0	0.0	6.7	0.0	6.7	0.0	46.7
Russia	79	30.4	6.3	16.5	22.8	7.6	6.3	0.0	10.1	0.0	46.9
Andreafsky	28	39.3	7.1	21.4	21.4	3.6	3.6	0.0	0.0	3.6	60.7
Kluane	27	44.4	7.4	7.4	37.0	0.0	0.0	0.0	3.7	0.0	81.4
Fishing Branch	28	10.7	3.6	14.3	64.3	7.1	0.0	0.0	0.0	0.0	75.0
Sheenjek	28	17.9	7.1	21.4	50.0	0.0	0.0	0.0	3.6	0.0	67.9
Tatchun	28	14.3	0.0	7.1	75.0	0.0	0.0	0.0	3.6	0.0	89.3
Yukon	139	25.2	5.0	14.4	49.6	2.1	0.7	0.0	2.2	0.7	74.8
Pallant	50	18.0	0.0	4.0	4.0	32.0	8.0	12.0	20.0	2.0	50.0
Fish Creek	46	10.9	4.4	0.0	10.9	37.0	8.7	10.9	10.9	6.1	47.9
Breezy Bay	40	27.5	2.5	5.0	12.5	10.0	10.0	12.5	10.0	10.0	37.5
Atnarko	24	29.2	0.0	4.2	8.3	41.7	0.0	4.2	12.5	0.0	70.9
North	160	20.0	1.9	3.1	8.9	29.4	7.5	10.6	13.8	4.9	49.4
Big Qualicum	58	8.5	0.0	1.7	1.7	16.9	37.3	8.5	23.7	1.7	45.8
Chemainus	24	16.7	0.0	0.0	0.0	4.2	37.5	4.2	37.5	0.0	54.2
Cowichan	22	4.6	4.6	4.6	4.6	13.7	31.8	4.6	22.7	9.1	36.4
Goldstream	23	13.0	4.4	0.0	8.7	13.1	30.5	13.1	13.1	4.4	43.5
Little Qualicum	24	37.5	0.0	0.0	0.0	12.5	16.7	0.0	33.3	0.0	54.2
Nanaimo	24	0.0	4.2	4.2	4.2	20.8	29.2	0.0	20.8	16.7	29.2
Puntledge	25	16.0	4.0	0.0	0.0	12.0	24.0	16.0	20.0	8.0	40.0
ECVI	200	13.0	2.0	1.5	2.5	13.9	30.8	7.0	24.4	5.0	43.8
Demamiel	23	17.4	0.0	0.0	0.0	4.4	26.1	17.4	34.8	0.0	34.8
Nitinat	47	23.4	0.0	4.3	6.4	23.4	19.2	2.1	14.9	6.4	25.5
Conuma	22	0.0	4.6	0.0	9.1	31.8	9.1	13.6	27.3	4.6	13.6
WCVI	92	16.3	1.1	2.2	5.4	20.7	18.5	8.7	22.8	4.4	25.0
Alouette	23	21.7	0.0	0.0	8.7	8.7	21.7	4.4	21.7	13.0	43.4
Chehalis	24	8.3	4.2	4.2	8.3	16.7	20.9	8.3	20.8	8.3	29.1
Chilliwack	48	16.7	0.0	2.1	18.8	12.5	18.8	6.3	16.7	8.3	33.4
Inch	21	0.0	0.0	4.8	14.3	4.8	47.6	4.8	19.1	4.8	19.1
Stave	21	4.8	4.8	0.0	0.0	28.6	28.6	0.0	33.1	0.0	37.9
Wahleach	22	4.6	0.0	13.7	0.0	7.6	27.3	18.2	18.2	13.6	22.8
Fraser	159	10.7	1.3	3.8	10.1	12.6	25.8	6.9	20.7	8.2	31.4
Mamquam	24	0.0	4.2	0.0	8.3	25.0	16.7	4.2	33.3	8.3	8.3
Tzoonie	22	9.1	9.1	0.0	0.0	18.2	9.1	9.1	45.5	0.0	9.1
Mainland	46	4.5	6.7	0.0	4.1	21.6	12.9	6.6	39.4	4.2	8.7

The simulations suggest that relatively accurate estimates of stock composition may be possible should minisatellite DNA variation be applied to practical fisheries management issues but that identification of individual fish to specific regions, particularly in North American stocks surveyed, is less accurate. For example, estimated Fraser River stock composition of pure samples of Fraser River chum salmon ranged from 87 to 93% when resolved with an 18-stock resampled southern British Columbia baseline, but only about 31% of individual Fraser River fish were correctly identified as of Fraser River origin when a 39-stock North Pacific baseline was used. About 26% of the Fraser River individuals were classified as originating from the east coast of Vancouver Island, a result which may seem in conflict with the greater separation observed between Fraser River and ECVI stocks in the estimation of mixture composition. However, estimation of stock composition of a mixture and classification of individual fish in the mixture are separate problems, with classification of individual fish the more difficult problem. Data from only a single fish that is to be identified are considered in classification problems, but data from all fish in the mixture as a whole are considered when estimates of stock composition are determined. Higher levels of accuracy (99%) have been observed previously in estimation of chum salmon composition by using the entire mixture sample rather than by classifying individual fish in the same mixture to region of origin (<60%) (Fournier et al., 1984).

Although analysis of minisatellite DNA variation may be an effective method for estimation of stock composition of chum salmon, a number of improvements would be required before it could be applied (either by itself or as an enhancement) to existing stock identification techniques for chum salmon. Determination of the allelic frequency distributions or band counts at the minisatellite loci for all stocks contributing significantly to fisheries, as well as ensurance that sampling of the contributing populations is adequate to represent samples of the stock that have been collected, would be required.

Genetic variation provides a powerful means to estimate stock composition of chum salmon catches. The particular method used to screen variation will depend on the issue to be resolved. Estimation of stock composition to large regional groups could be conducted with analysis of variation at protein-coding loci, in mitochondrial DNA, in minisatellite DNA, or in the major histocompatability complex (MHC) genes (Miller and Withler, in press). Estimation of local stock composition to a fine scale, such as to tributaries of a major river system, will likely require direct measurement of DNA variation. Surveys of variation at minisatellite loci provide one possibility of achieving fine-scale estimation of stock composition, but analysis of variation at other minisatellite loci, in addition to those utilized in the current manuscript, will be required. No surveys of population variation at microsatellite loci for chum salmon have been conducted yet, although there may be great potential in their application (e.g. Brooker et al., 1994). Given the relative ease of laboratory analysis of variation at microsatellite loci, compared with that at minisatellite loci, microsatellite loci may be more practical than minisatellite loci, on a routine basis, for stock-identification analysis.

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The reproductive condition of white sturgeon, *Acipenser transmontanus*, in San Francisco Bay, California

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Abstract.—White sturgeon, *Acipenser transmontanus*, adults (n=855) were collected on their feeding grounds in San Francisco Bay, California, and their sex and stage of sexual maturity were evaluated histologically. They did not exhibit external sexual dimorphism, and the overall sex ratio did not differ from 1:1. Average fork length was 139 cm ±1.1 cm (mean ± standard error of the mean); females were longer (145 cm ±1.2 cm, n=443) than males (133 cm ±1.0 cm, n=412). In smaller size classes (≤115 cm), males were significantly (P<0.05) more numerous than females. The proportion of females, however, was significantly higher among larger fish (>155 cm). The sample of females consisted of 70% fish with "immature" (previtellogenic) ovaries, 12% with "maturing" (vitellogenic) ovaries, and 18% with "ripe" (large, pigmented eggs) ovaries. In contrast, most males were either "maturing" (meiosis, 56%) or "ripe" (spermatozoa, 39%). Ripe females represented only 9% of all fish sampled. Egg production by females, estimated by hatchery spawning, averaged 5,648 eggs/kg of body weight. The length at which white sturgeon in San Francisco Bay attain sexual maturity was estimated to be 95–135 cm in females and 75–105 cm in males. The duration of one ovarian cycle in iteroparous females was estimated to be longer than one year, with an apparent 2- to 4-year interval between spawning periods; the reproductive cycle of males was estimated to be 1–2 years. The low reproductive potential of white sturgeon in San Francisco Bay should be considered in fishery management of the species.

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White sturgeon, *Acipenser transmontanus*, have long been valued for their caviar and flesh for human consumption. Recently white sturgeon have become popular as a recreational fish (Galbreath, 1985; Kohlhorst et al., 1991) and are being raised by commercial aquaculturists (Logan et al., 1995). During the last four decades, researchers have gathered sufficient information on the biology of wild populations to improve management of the fishery. Information now exists on white sturgeon migratory patterns (Miller, 1972; Kohlhorst et al., 1991), feeding habits (Schreiber, 1962; Semakula and Larkin, 1968; McKechnie and Fenner, 1971; McCabe et al., 1993), age, growth, and population structure (Semakula and Larkin, 1968; Kohlhorst et al., 1980; Brennan and Cailliet, 1991; Kohlhorst et al., 1991; DeVore et al.[1]). Significant knowledge exists on their reproduction, including gonadal development (North et al.[2]; Welch and Beamesderfer[3]), natural spawning (Stevens and Miller, 1970; Kohlhorst, 1976; Parsley et al., 1993; McCabe and Tracy, 1994), gamete and fertilization biology (Cherr and Clark, 1985), and early development (Beer, 1981; Wang et al., 1987; Bolker, 1993).

White sturgeon are anadromous and endemic to Pacific estuaries and coastal rivers of North America. They are found from the Aleutian Islands of Alaska to Monterey Bay, California (Scott and Crossman, 1973). In the Pacific Northwest, they are most abundant in the Fraser, Columbia, and Sacramento–San Joaquin rivers. The San Fran-

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cisco Bay estuary has the largest population of white sturgeon in California. Adults spend most of their life in the bay and migrate into the Sacramento River in the late winter or early spring to spawn (Pycha, 1956; Stevens and Miller, 1970; Kohlhorst, 1976). White sturgeon are believed to reach sexual maturity at age 10 to 30 years, and iteroparous females spawn at intervals of two or more years (Pycha, 1956; Semakula and Larkin, 1968).

We focused our initial studies on the collection of wild broodstock for captive breeding in order to develop artificially induced spawning techniques and hatchery technology (Conte et al., 1988). Concomitantly, we sampled white sturgeon in San Francisco Bay in order to characterize the composition of the population in relation to sex and gonadal maturity.

Materials and methods

White sturgeon were collected in the San Francisco Bay estuary, California, from late October to February 1983–86. The fishing grounds included the area between Golden Gate Bridge, Angel Island, and San Francisco Bay Bridge. Miller (1972) observed that sturgeon congregate in this area to feed and that fish that were ripe migrated into the Sacramento River later in the season to spawn. Sturgeon aggregated while feeding on herring eggs and were seen frequently jumping out of the water. These aggregations of sturgeon were located with sonar. Fishing gear consisted of a short (167–214 cm) stiff pole (rated for 28 kg) equipped with reel (4/0), heavy monofilament line (18–28 kg strength), leader (45–55 kg strength), treble hook (4/0 or 5/0), and heavy sinker (142–227 g). The line was weighted with a sinker at the end of the leader, and the treble hook was attached approximately 30 cm above the sinker.

Sturgeon were usually encountered at water depths of 6 to 9 m and were snagged as they rubbed the line or hooked when they took a bait of herring fillet or eggs. Water temperatures and salinities during collection periods were 9–15°C and 24–32 ppt, respectively. Further details on fish-collection techniques are described and illustrated by Cuanang (1984). White sturgeon broodstock handling, sampling, and care followed procedures of Conte et al. (1988).

Sturgeon were examined for external structure and size, including morphometric and meristic characters. Measurements included fork and total length (±0.1 cm), head length (±0.1 cm), mouth width (including the lips, ±0.1 cm), and body weight (±0.1 kg). Meristic characters of the scutes in the dorsal, lateral, and ventral rows were recorded according to the methods of Vladykov and Greeley (1963). Proportional measurements (snout and head) were expressed as percentages of the head and fork length, respectively. Sturgeon were alive when sampled, and all fish, except for ripe broodstock, were released after capture. Samples of gonadal tissue and blood plasma were collected for histological analysis, but sections of fin rays were not collected for age determinations in order to avoid excessive trauma.

Sex and stages of sexual maturity in white sturgeon were examined by using histological slides of gonadal tissue and light microscopy (Chapman, 1989; Doroshov et al., 1991). Gonadal samples were collected from 300 females and 325 males. Ovarian stages in females were assigned a numerical score according to differentiation in the shape and size of the ovarian follicle (according to oocyte cytoplasm staining properties, nuclear and cytoplasmic inclusions, presence or absence of yolk platelets, differentiation of the vitelline envelope, and differentiation in the granulosa cells and thecal follicular layers). A numerical score was assigned to each male testis according to the proportion of cysts with different types of germ cells that were counted in several random fields on the slide (spermatogonia, spermatocytes, spermatids, and spermatozoa). Based on histological scores, the following classification was assigned for individual fish: (1) "immature," (2) "maturing," or (3) "ripe." Group-1 fish included females in the previtellogenic stage of ovarian development (in chromatin nucleolar stage and primary oocyte growth) and males in the gonial proliferation stage of testicular development. Group-2 fish included females with ovaries in early or intermediate phases of vitellogenesis (oocyte cytoplasm containing yolk bodies) and males with testes in the meiotic phase (spermatocytes and spermatids). Group-3 fish included females with ovaries containing large and darkly pigmented oocytes exhibiting yolk polarization and germinal vesicle migration and males in the postmeiotic testicular phase (spermiogenesis and differentiated spermatozoa).

Data on egg production (approximate individual relative fecundity) were collected from gravid females that had been captured in the Sacramento River from February to March 1991–94 in order that they might spawn in the hatchery. Estimation of egg production was based on the number of eggs collected surgically (a procedure routinely performed during artificial spawning of sturgeon [see Conte et al., 1988]) and represents 60–80% of actual individual fecundity.[4] The number of eggs removed from each female was

[4] The percentage of eggs collected was determined by comparing egg production at spawning of domestically raised sturgeon with a total fecundity estimate of domestic sturgeon (of equivalent size) processed for caviar production.

estimated volumetrically by using three 5-mL volume subsamples. Egg diameters were measured (±0.01 mm) along the animal-vegetal axis with a dissecting microscope and ocular micrometer.

Procedures described in Steel and Torrie (1986) were followed for statistical analyses. The Statistical Analyses System software (SAS, 1985) was used for data processing. The measure of variability is reported as standard error of the mean (±SEM), and the accepted level of statistical significance is $P<0.05$. All length measurements are given in fork length (FL).

Results

Body size, sex ratio, and sexual dimorphism

We sampled a total of 855 white sturgeon, ranging in fork length from 79 to 202 cm (mean=139 ±1.1 cm). Mean length of females (145 ±1.2 cm) was significantly greater than that of males (133 ±1.0 cm). The sex ratio was 1:1 (Table 1). The proportion of males, however, was significantly higher among fish ≤115 cm, whereas the proportion of females was higher among fish >155 cm (Table 1).

In most cases we could not determine by external examination the sex of white sturgeon, except for spermiating males and some ripe females (recognized by an enlarged abdomen). We found no significant differences between the sexes in numbers of dorsal and lateral scutes, relative lengths of the head and snout, and width of the mouth. Among all fish examined histologically, we found only one case of hermaphroditism, a maturing testis containing a few ovarian follicles with previtellogenic oocytes.

Table 1

Size classes and sex ratios of white sturgeon, *Acipenser transmontanus*, sampled in San Francisco Bay, California, from October to February, 1983–86. Significant deviations (chi-square) from the expected 1:1 sex ratio are marked by asterisks.

	Sample size			
Fork length (cm)	Total	No. of males	No. of females	Sex ratio
<95	14	9	5	0.64:0.36*
95.1–105	84	53	31	0.63:0.37*
105.1–115	119	79	40	0.66:0.34*
115.1–125	120	59	61	0.49:0.51
125.1–135	109	57	52	0.52:0.48
135.1–145	135	58	77	0.43:0.57
145.1–155	93	46	47	0.50:0.50
155.1–165	87	33	54	0.38:0.62*
165.1–175	56	12	44	0.21:0.79*
>175	38	6	32	0.16:0.84*
Total	855	412	443	0.48:0.52

Distribution of maturity stages in the population

The smallest ripe female and male were 104 cm and 100 cm, respectively. The female sample population comprised 70% group-1, 12% group-2, and 18% group-3 individuals (Table 2). Except for one large size class (175.1–185 cm), the proportion of immature females remained high (>62%) in each length class. Although females with vitellogenic or ripe ovaries (groups 2 and 3) appeared in length classes 95.1 to 125.1 cm, their proportions were small (average 3% for group 2 and 6% for group 3). In 135.1–195 cm sturgeon, the proportions of females with maturing and ripe

Table 2

Proportions of gonadal maturity stages in different size classes of white sturgeon females (n=300) and males (n=325) in San Francisco Bay, California.

Female size class (cm FL)	Number in sample	Female gonadal maturity stage (%)		
		Group-1	Group-2	Group-3
75.1–85	1	1.00	0.00	0.00
85.1–95	1	1.00	0.00	0.00
95.1–105	9	0.89	0.00	0.11
105.1–115	28	0.96	0.00	0.04
115.1–125	31	0.90	0.03	0.07
125.1–135	33	0.88	0.06	0.06
135.1–145	34	0.65	0.15	0.20
145.1–155	47	0.66	0.13	0.21
155.1–165	45	0.56	0.13	0.31
165.1–175	39	0.62	0.15	0.23
175.1–185	22	0.27	0.32	0.41
185.1–195	10	0.70	0.20	0.10
Male size class (cm FL)	Number in sample	Male gonadal maturity stage (%)		
		Group-1	Group-2	Group-3
75.1–85	2	0.50	0.50	0.00
85.1–95	1	0.00	1.00	0.00
95.1–105	18	0.33	0.50	0.17
105.1–115	52	0.10	0.59	0.31
115.1–125	59	0.04	0.64	0.32
125.1–135	54	0.04	0.54	0.42
135.1–145	51	0.02	0.63	0.35
145.1–155	37	0.00	0.49	0.51
155.1–165	33	0.00	0.45	0.55
165.1–175	12	0.00	0.42	0.58
175.1–185	3	0.00	0.67	0.33
185.1–195	3	0.00	0.67	0.33

ovaries (groups 2 and 3) increased and stabilized at an overall average of 16% (= 32/197) in group 2 and at a overall average of 25% (= 50/197) in group 3; the remaining 59% consisted of group-1 females. The average proportion of ripe females (group 3) in size groups less than 135.1 cm was statistically less than that observed in the combined size class of 135.1 to 195 cm (chi-square, $P<0.05$). A similar result holds for maturing (group-2) females (chi-square, $P<0.05$). Together, these data indicated that proportions of reproductively active females in the sturgeon population may be determined by a combination of two factors: 1) the recruitment of females into puberty (first vitellogenic cycle) occurs over a range of body sizes beginning at 95.1 cm; and 2) female white sturgeon require more than a one-year interval between consecutive spawnings. If one conjectures a predominant 4-year spawning period in iteroparous females (because of the percentage [25%] of ripe females), we could expect to see a ratio of immature to mature to ripe around 2:1:1 in size classes above 135 cm. Our data reject this ratio (chi-square, $P<0.005$). Unfortunately, we were not able to clearly distinguish between the first and second spawning cycles by histological examination of vitellogenic and ripe ovaries.

Male samples, in contrast to female samples, had overall low proportions of immature (premeiotic phase) individuals (5% in group 1), and recruitment into the meiotic phase of spermatogenesis (group 2) occurred at a smaller size, beginning at 75.1 cm (Table 2). Sampled fish from 105.1 to 195 cm were practically all (294 of 304) in group 2 (57%) or group 3 (40%). If one conjectures a predominant biennial spawning interval, we would expect the data to show a 1:1 ratio of meiotic and postmeiotic testicular stages. Our data reject this ratio (chi-square, $P<0.001$).

Relative fecundity (egg production)

Egg production from artificially spawned wild white sturgeon females ranged from 3,192 to 8,582 eggs/kg of body weight. The average size of ova was 3.7 mm ±0.02 mm. The average weight of these females was 36 ±2 kg and fork length was 153 ±4 cm (n=40). The estimated hatchery production was 203,328 ova for a female of average size; individual fish produced between 63,840 and 469,432 eggs. The relationship between the egg diameter and fork length was not statistically significant.

Discussion

We found that white sturgeon do not have external sexual dimorphism and, except for ripe fish on spawning grounds, there are no apparent morphological differences between the sexes. The 1:1 sex ratio (overall) of white sturgeon in San Francisco Bay is in agreement with data for the Columbia River system (Beamesderfer and Rien[5]) and Eurasian acipenserid species (Chugunov and Chugunova, 1964; Zubova, 1971; Persov, 1975). A greater proportion of males in smaller size classes and a predominance of females in larger size classes have also been observed in other species of sturgeon (e.g. *A. sinensis*, Xin et al., 1991). One possible explanation for this difference in sizes is that growth rates diverge between the sexes during the reproductive phase of life. Kohlhorst et al. (1980) found no difference in growth rates between sexes in white sturgeon of the San Francisco Bay; however, their study was limited to a narrow size and age range. An alternative explanation may be a higher rate of mortality in males and a resultant shorter life span in comparison with females. High rates of mortality for males may be associated with earlier puberty, more frequent breeding, and longer residence on the spawning grounds. Assuming that the population was sampled randomly, both differences in growth and mortality may have contributed to the substantial divergence in modal size classes between the males (105.1–115 cm FL) and females (135.1–145 cm FL). Although the predominance of females among larger fish may be explained by these factors, the predominance of males among smaller fish appears to contradict a chromosomally determined (gonochoristic) sex ratio and should be investigated further.

Although subject to high individual variation, the relative fecundity among sturgeon species appears to be generally similar. For example, for the large anadromous species *Huso huso*, Raspopov (1987) reported a relative fecundity of 2,750 to 10,500 eggs/kg of body weight. Smaller species such as shortnose sturgeon, *A. brevirostrum*, had an average relative fecundity of 11,568 eggs/kg of body weight (Dadswell, 1979). Although we could not directly estimate relative fecundity for white sturgeon females in San Francisco Bay, egg production from artificially spawned females averaged 5,648 eggs/kg of body weight and 203,328 eggs for an average length (153 cm) female. Relative fecundity for white sturgeon females in the Columbia River was not reported; however, the number of eggs produced was from

[5] Beamesderfer, R. C., and T. A. Rien. 1993. Dynamics and potential of white sturgeon populations in three Columbia River reservoirs. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol.1, report H, p. 175–204. Final Report (Project 86-50) to Bonneville Power Admin., Portland, Oregon.

98,200 to 699,000 eggs for fish 115 to 215 cm FL (DeVore et al.[1]). Comparisons of egg diameters in ripe females from the Sacramento and Columbia rivers revealed that female sturgeon from the Sacramento River had larger eggs (3.4–4.0 mm) than those found in females from the Columbia River (2.6–3.6 mm) (North et al.[2]). This difference may account for the apparent higher fecundity of white sturgeon females in the Columbia River. We found no relation between size of the female sturgeon and mature egg diameters. Lutes et al. (1987) also did not detect a relation between female body size and diameters of postvitellogenic oocytes in white sturgeon.

The size at which white sturgeon attain sexual maturity appears to vary between populations. Our observations indicate that female white sturgeon in San Francisco Bay mature at larger sizes (>95 cm) than males (>75 cm). Because the proportions of ripening individuals (groups 2 and 3) increased and stabilized above 135 cm in females and 105 cm in males, recruitment into puberty most likely occurs from 95 to 135 cm for females and from 75 to 105 cm for males. In the Columbia River, female white sturgeon did not mature until they were even larger (160–193 cm FL), revealing significant size variations in the river downstream from all dams and between different river reservoirs (DeVore et al.[1]; Welch and Beamesderfer[3]; Beamesderfer and Rien[5]). These differences in size at first sexual maturity were largely attributed to food availability and hydrologic conditions. Working with wild and domestic stocks, Chapman (1989) postulated that size and age at sexual maturity in white sturgeon were dependant on body size and nutrient composition. Size or age at sexual maturity, however, could be modified by growth, nutrition, and environmental factors.

Examination of the stage of gonadal development in different length classes of white sturgeon females in San Francisco Bay indicated a high fraction of group-1 (immature) individuals. The proportions of group-2 (maturing) and group-3 (ripe) females in the sampled population were low (12% and 18%, respectively); ripe females represented only 9% of all sturgeon sampled. Similar observations in the Columbia River system revealed even lower proportions, 6% maturing and 2% ripe (DeVore et al.[1]; North et al.[2]; Welch and Beamesderfer[3]). From histological analysis of oogenesis (Chapman, 1989) and from the proportions of different ovarian stages in the white sturgeon population of San Francisco Bay, we assume that iteroparous sturgeon females require longer than one year to complete an egg development cycle, including vitellogenic growth and prematurational polarization of the oocyte. Because the proportion of females with ripe ovaries (group 3, >135 cm) was on average 25% of all sampled individuals, the interval between two consecutive spawnings is most likely between 2 and 4 years. Our recent observations of domestically raised and continuously fed white sturgeon suggest predominantly biennial ovarian cycles. Because wild female sturgeon, compared with other fish including domestic sturgeon, lose a substantial percentage of weight and energy at spawning (Krivobok and Tarkovskaya, 1970), it is possible that they defer a new wave of ovarian vitellogenesis for some time after spawning, allowing recovery from spawning depletions (the high percentage [59%] of fish in group 1 strongly suggests this event). A final conclusion regarding spawning periodicity of white sturgeon cannot, however, be reached until fish that have been tagged are recaptured and sampled repeatedly or until the size and age interval of female recruitment to puberty is known. These are important considerations, because pubertal age of white sturgeon females may extend from 15 to 32 years (White Sturgeon Planning Committee[6]).

Considering the season of our sampling (late fall–early winter) and the potential overlap between meiotic and maturational phases of testicular development, the adult male white sturgeon may spawn annually (as in commercial hatcheries) or biennially. Existence of a biennial cycle in sturgeon males could be verified by continued sampling throughout spring and summer. Most spawning males accommodate the protracted spawning season (February–June) of females. This shorter reproductive cycle, which is associated with annual spawning migrations, may also result in a higher mortality for older and larger males.

A 2–4.5 year spawning period has been suggested for female white sturgeon in the Columbia River (Welch and Beamesderfer[3]). According to Trusov (1975), the refractory ovarian stages in iteroparous sevryuga, *A. stellatus*, last 2 to 5 years, whereas the ovarian vitellogenesis occurs within 1 to 2 years. Examining the sexual maturation of Russian sturgeon, *A. guldenstadti*, in the Sea of Azov, Kornienko et al. (1988) found that 72% of the sampled adult-size fish had either immature or refractory ovaries and that the remaining fish were approximately equally distributed between "maturing" and "ripe." In males, spermatogenesis was a continuous process.

We conclude that sexual maturation in white sturgeon is prolonged. Females mature slowly, and first maturation takes place over a wide range of body sizes. The average interval between spawnings by iteroparous females appears to range from 2 to 4

[6] White Sturgeon Planning Committee. 1992. White sturgeon management framework plan. 2501 S.W. First Avenue, Pacific States Marine Fisheries Commission, Gladstone, Oregon.

years. Males mature at a smaller body size and have shorter intervals between spawnings than do females. Sex differences in maturation rates of sturgeon create incredible combinations of individual matings from different generations that favor genetic diversity even with a small number of spawning females. Annual recruitment and genetic structure of a sturgeon population may be influenced by its sex ratio, the proportion of females spawning each year, and the number of eggs they produce. Monastyrski (1949) noted that the complex age-size structure of spawning populations and the iteroparity of sturgeons require a special approach for their management. Our data on the reproductive conditions of white sturgeon in the San Francisco Bay provide additional evidence for potential sensitivity of sturgeon populations to exploitation by either commercial or sport fisheries. The effect of prolonged sexual maturation may be compromised further by loss of spawning habitat, altered seasonal changes of temperature in rivers with controlled flow, and environmental pollutants that may affect sexual development and the reproductive cycle.

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Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States*

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Abstract.—The vermilion snapper, *Rhomboplites aurorubens*, is an important species in headboat and commercial reef fisheries in the southeastern United States, especially in the Carolinas. The reproductive biology of vermilion snapper was determined from samples collected on biweekly research cruises (April to August 1992 and May 1993) and from samples collected from commercial vessels (September to April 1992–93). Vermilion snapper did not exhibit a 1:1 sex ratio; 63% of the specimens were female. The reproductive season of vermilion snapper is April through late September in the southeastern United States. All vermilion snapper examined were mature, with the smallest female at 165 mm FL, the smallest male at 179 mm FL. The smallest fish aged (165 mm FL) was two years old. Length was the best predictor of batch fecundity ($BF=0.0438FL^{2.508}$). Vermilion snapper spawn approximately every five days or about 35 times a year. Atresia did not significantly affect fecundity estimates. Vermilion snapper is an indeterminate spawner; its oocytes mature continuously during the spawning season and there is no hiatus between the size distribution of the oocyte classes. Total fecundity did not decline over the spawning season. Rather, it gradually increased through August and then declined in September. Mean oocyte diameter stayed constant over the reproductive season. The order of spawning batches was not consistent with the determinate fecundity prediction.

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The vermilion snapper, *Rhomboplites aurorubens*, is a small lutjanid distributed from North Carolina and Bermuda, through the West Indies and the Gulf of Mexico, and south to southeastern Brazil (Böhlke and Chaplin, 1968). It is associated with two distinct habitats on the outer continental shelf near the Carolinas: shelf-edge habitat (64–183 m) and inshore "live-bottom" habitat (26–56 m) (Grimes, 1976). This lutjanid attains a maximum total length of approximately 600 mm (24 in) and a maximum weight of 2.8 kg (6 lb) (Grimes, 1978).

Vermilion snapper is an important species in the headboat and commercial reef fish fisheries of the Carolinas. Despite an increase in landings in North Carolina, South Carolina, and Georgia from 6.8 metric tons (t) (15,000 lbs) in 1988 to 499 t (1.1 million lbs) in 1991, catch per unit of effort (CPUE) exhibited a marked decline (Zhao and McGovern[1]); there was also a significant decrease in mean length of vermilion snapper taken by fishery independent sampling and by headboat and commercial fisheries (Collins and Sedberry, 1991; Zhao and McGovern[1]) over the same period.

Declines in CPUE and mean size in fishery-independent samples indicate that vermilion snapper is overfished (Collins and Sedberry, 1991). Owing to the importance of vermilion snapper in the southeastern U.S. fisheries, current information on all aspects of its reproduction is needed to manage the vermilion snapper fishery effectively. Fecundity and sexual maturity information is essential for management of any fishery of economic consequence to a region (Hunter et al., 1992). Fecundity data are needed to calculate a spawning stock ratio (SSR) in annual stock assessments for use in evaluating management regulations. To quantify fecundity

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[1] Zhao, B., and J. C. McGovern. 1996. Population characteristics of the vermilion snapper, *Rhomboplites aurorubens*, from the southeastern United States. In preparation.

and spawning frequency more accurately, new techniques, such as the hydrated oocyte method for fecundity estimates (Hunter et al., 1985) and the postovulatory follicle method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985) for determining spawning frequency, need to be used. There is considerable information on the reproductive biology of over 40 lutjanids (Grimes, 1987); however, there is only one recent study (Davis and West, 1993) that uses the new assessment methods on a lutjanid.

Recent studies of the reproductive biology of vermilion snapper in the southeastern U.S. are quite limited. Current management of the vermilion snapper fishery is based on age, growth, and reproductive data collected in the early to mid-1970's, prior to the rapid expansion of the fishery (Grimes, 1978; Grimes and Huntsman, 1980). Grimes (1976) and Grimes and Huntsman (1980) examined aspects of the reproductive biology of vermilion snapper in this area in the early 1970's, but neither used a histological technique to assess reproductive season, spawning frequency, or maturity. Collins and Pinckney (1988) reported on the maturity of vermilion snapper in the southeastern United States from 1978 to 1980 but used only scales to age fish. The reproductive biology of vermilion snapper has also been studied in the Gulf of Mexico. Nelson (1988) examined the sex ratio, size at maturity, spawning frequency, and fecundity of vermilion snapper off Flower Garden Banks, Gulf of Mexico, from 1980 to 1982 but did not use a histological technique. These data need to be supplemented with more recent information, including histological criteria and more accurate assessment methods.

Although vermilion snapper is considered a multiple spawner on the basis of its prolonged spawning season, variation in the gonadosomatic index for similarly sized fish, and variation in the number of maturing ova types found in the ovary (Grimes and Huntsman, 1980), a reassessment of the reproductive biology of vermilion snapper, using recently developed techniques, is necessary 1) to quantify the annual reproductive cycle; 2) to determine age and size at maturity and to detect changes that may have occurred because of the fishery; 3) to estimate spawning frequency; 4) to describe vermilion snapper as either a determinate or indeterminate spawner; and 5) to calculate fecundity (corrected for atresia) of the vermilion snapper in the southeastern United States.

Materials and methods

Specimens were obtained between April 1992 and May 1993 on research cruises conducted as part of a fishery-independent survey of reef fishes. Scientists of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program (see Collins and Sedberry [1991] and Zhao and McGovern[1]) conducted biweekly cruises to randomly selected reef sites, from Cape Lookout, North Carolina, to Jacksonville, Florida (Fig. 1). Sampling in 1992 was conducted from April through August, and in 1993 from May through August by using baited chevron-shaped (arrowhead) fish traps (Collins, 1990) soaked for 90 min during daylight only. The time of trap deployment was recorded as time of catch. Some (n=24) fish were collected with hook-and-line gear fished at dawn or dusk (Collins and Sedberry, 1991). Measurements taken from the vermilion snapper catches were lengths in mm (total length [TL] and fork length [FL])

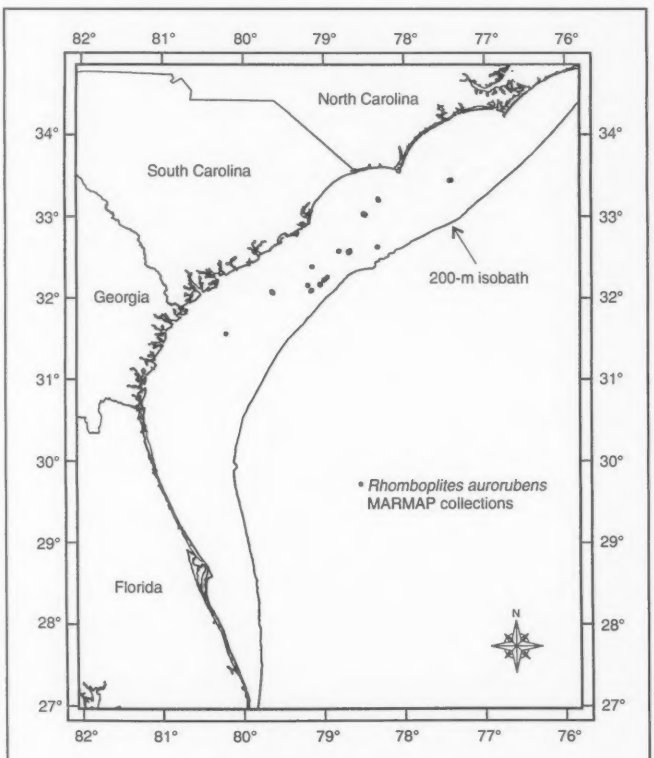

Figure 1

MARMAP station locations of vermilion snapper, *Rhomboplites aurorubens*, captured from April to August 1992 and in May 1993. (n=110)

and weights (g/total body weight and g/ovary-free body weight [OFWT] ±1 g) . Ovaries were removed, blotted dry, and weighed and fixed in 10% buffered seawater formalin. After fixation, samples of ovarian tissue were weighed with an Ohaus digital balance (±0.001 g) for fecundity determination. Conversion factors were developed for samples taken during the first three months of the study because fresh gonad weight and OFWT were not measured. When sampling was not untertaken (September to April), additional samples were purchased from the commercial hook-and-line catch landed in Georgetown, South Carolina. Commercial samples were used for histological examination (see below), both to define the spawning season and to gather atresia measurements.

A modified gonadosomatic index (GSI) was used to quantify the reproductive cycle. The GSI was calculated as $GSI = (gonad\ weight/OFWT) \times 100$ (Nieland and Wilson, 1993; Nikolsky, 1963). In order to make comparisons with the findings of Grimes (1976), the following gonad index (GI) equation was used:

$$K_G = (WT_G / TL^3) \times 10^6,$$

where WT = preserved weight of the gonad (g), and
TL = total length (mm).

GI values from Grimes (1976) were compared with GI values from the present study to evaluate possible differences between the two studies in reproductive timing and size and age at maturity.

A chi-square test was used to evaluate the sex ratio of vermilion snapper. A 2×2 contingency table was used to compare the sex ratios in Grimes (1976) with those in the present study and to compare MARMAP samples with commercial samples (Zar, 1984). Sex-ratio data were also analyzed by 50-mm length classes by using a 2×4 contingency table (Zar, 1984)

Histological analysis was used to assess maturity and spawning activity and to verify whole-oocyte staging. Gonad sections were prepared according to the methods of Wenner et al. (1986). The developmental stage of each ovary was identified by using the criteria of Hunter et al. (1992) (Table 1). Each ovary was also examined for the presence or absence of the two stages of postovulatory follicles (POF's). Testes were classified by means of the modified criteria of Wyanski and Pashuk[2] (Table 2).

Maturity definitions I–V from Hunter et al. (1992) were used to classify females. Mature females included the following: all active females; all inactive mature females; inactive females with early yolked oocytes and with alpha, beta, or no atresia; and inactive females with unyolked oocytes and with alpha or beta atresia (Table 1). If testes were developing, ripe, spent, or resting, they were considered mature (Table 2).

Transverse sections of otoliths were made with a Buehler Isomet low-speed saw. Sections were mounted on slides, immersed in cedarwood oil, and viewed under a dissecting microscope. The dissecting microscope was linked by a video camera to a MATROX frame grabber and personal computer with OPTIMAS image analysis software.

The following fecundity definitions from Hunter et al. (1992) were used in the present study:

Determinate fecundity	Annual fecundity is fixed prior to the onset of the spawning season.
Indeterminate fecundity	Annual fecundity is not fixed prior to the onset of the spawning season, and unyolked oocytes continue to mature and are spawned during the spawning season.
Annual fecundity (AF)	Total number of eggs spawned per year.
Total fecundity (TF)	Standing stock of advance-stage yolked oocytes (AYO's).
Potential fecundity (PF)	Total AYO's that mature per year. Potential fecundity was considered to be equivalent to the standing stock of AYO's in fully developed prespawning females.
Batch fecundity (BF)	Total number of hydrated oocytes (HO's) released in one spawning.

If vermilion snapper is a determinate spawner, then the following are expected: a hiatus will develop in the frequency distribution of oocyte diameter between the oocytes that mature for the season and the reservoir of less advanced oocytes present year round; TF declines over the spawning season; mean oocyte diameter (MOD) increases over the spawning season; and the spawning order of batches is consistent with the determinate fecundity definition (see Hunter et al., 1992).

To determine whether AYO's were randomly distributed throughout the ovary, the densities of AYO's at six locations within the ovaries of nine fish were

[2] Wyanski, D. M., and O. Pashuk. 1996. Processing and interpretation of fish reproductive tissue at the Marine Resources Research Institute of the South Carolina Department of Natural Resources. In preparation.

compared. The locations were anterior, center, and posterior in both the left and right lobes of the ovary. A wedge from the exterior of the ovary to the interior of the ovary was taken for each location sampled. A two-way ANOVA was run to test for effects of location and individual fish on oocyte density.

Whole oocytes were staged by using the criteria of Hunter et al. (1992). Yolk density was used to discriminate between the different developmental stages of oocytes, with counts of stage-3 AYO's (Fig. 2A) being the basis of TF estimates. The definitions of each stage were as follows:

Stage 1 Initial layer of yolk along the periphery of the oocyte appearing as a narrow band but not extending over 20% of the distance

Table 1

Histological stages of female vermilion snapper, *Rhomboplites aurorubens*, modified from Hunter et al. (1992).

Inactive	Active
Not capable of spawning now or in the near future.	Capable of spawning now or in the near future. Ovary contained enough advanced yolked-oocytes (AYO's) for one spawning.
Mature Ovaries show clear evidence of past spawning or past maturation of AYO's.	**Mature** AYO's present with no or minor (<49%) alpha atresia of AYO's.
Postspawning. Contains either postovulatory follicles (POF's) and no AYO's, or contains POF's with mostly atretic AYO's.	Spawning. Evidence of past spawning (POF's) or imminent spawning (hydrated oocytes [HO's]) or migratory nucleus-stage oocytes (MNO's).
Major atresia. AYO's present, alpha atresia of AYO's ≥50%.	Nonspawning. No evidence of recent or imminent spawning, but fish are capable of spawning in the near future.
Uncertain maturity No AYO's present.	
Early yolked. Early yolked oocytes present. May have alpha, beta, or no atresia of early yolked oocytes.	
Unyolked. Unyolked oocytes present. Alpha or beta atresia of unyolked oocytes evident.	
Immature Unyolked oocytes present with no atresia.	

Table 2

Histological staging of male vermilion snapper following modified criteria developed by Wyanski and Pashuk (1990).

Inactive	Active
Not capable of spawning now or in the near future.	Capable of spawning now or in the near future.
Mature Spent. No spermatogenesis; some residual sperm in tubules and lumina.	**Mature** Developing. A few primary and secondary spermatocytes through tubules and lumina (no spaces) with spermatozoa.
Resting. Large cross section compared to immature male; little or no spermatocyte development; empty tubules and lumina evident.	Ripe. Predominance of spermatozoa; areas of spermatogenesis toward outer surface of testes in some specimens.
Immature Small cross section compared to resting male; little or no spermatocyte development; empty tubules and lumina not evident.	

between the nucleus and the zona pellucida (egg diameter ~0.15–0.25 mm)

Stage 2 Lightly packed yolk possibly extending from the periphery to the nucleus with the nuclear area still evident (~0.25–0.35 mm)

Stage 3 Yolk dense enough to occlude the nucleus (~0.35–0.45 mm)

Stage 4 Parts of the dense yolk become translucent usually beginning at the periphery (~0.45–0.60 mm)

Stage 5 Oocyte is translucent except for the oil droplet (~0.60–1.25 mm).

Alpha-atretic AYO's were not included in TF estimates.

To estimate total fecundity, whole oocytes were examined by using a modified version of the hydrated oocyte method of Hunter et al. (1985). Each sample weighed approximately 50 mg and consisted of about 100 to 150 oocytes. Three diameter measurements per oocyte were taken and then averaged to obtain a mean oocyte diameter (MOD). A mean of the MOD's of all AYO's in the two samples taken from each female was calculated for 138 females and then analyzed for TF. Oocytes on each gridded slide were counted, measured, and staged with GLOBAL LAB image analysis software linked by a video camera system to a compound microscope. The following fecundity equation was used to assess TF:

$$TF = Z \times C,$$

where Z = ovary weight in grams, and
C = oocyte density (number of AYO's per gram of ovarian tissue).

To see if time had an impact on TF, TF was regressed on OFWT and on days elapsed since 15 April. Also, an ANCOVA was performed on monthly TF regression equations to see if there was a temporal effect on TF.

To see if atresia had any effect on fecundity estimates, the proportion of atretic oocytes was calculated for each whole oocyte sample that was counted. The number of alpha atretic AYO's in a sample was divided by the total number of AYO's in that sample (Hunter et al., 1992). Atresia subclasses were defined by Bretschneider and Duyvene de Wit (1947) and Hunter and Macewicz (1985). Alpha atresia involves the reabsorption of the entire oocyte, and beta atresia involves the major degeneration and reabsorption of the follicle (Hunter and Macewicz, 1985). Three subclasses of alpha atretic AYO's were noted: no atresia, minor atresia (1–49%), and major atresia (50–100%).

To estimate PF, only females from the beginning of the spawning season that showed no recent signs of spawning (presence of HO's or POF's) were used in analyses. Because PF is estimated at the beginning of the season, some oocytes may not have yet been recruited into the stock of advanced yolked oocytes. To find the size at which oocytes are fully recruited, a series of stepwise multiple regressions was run on 59 females (Table 3). Data were removed by 0.005 mm increments beginning with the lowest diameter class of 0.360 mm. Analysis indicated that the threshold for a significant effect of diameter on PF occurred between 0.445 mm and 0.450 mm. The regression coefficient for oocyte diameter was significant for females with a MOD equal to or less than 0.445 mm but insignificant for females with a MOD

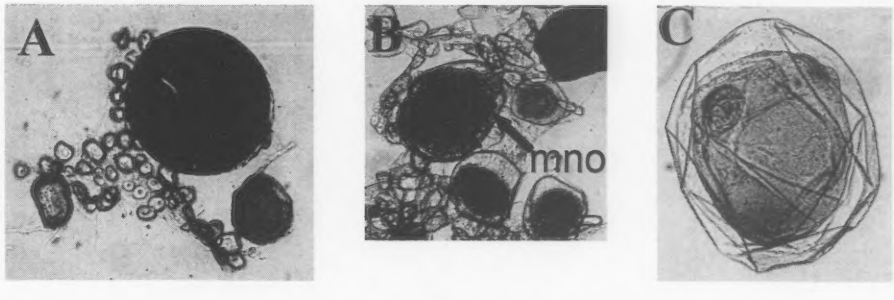

Figure 2

Photographs of whole oocytes of vermilion snapper at 40×: (**A**) stage-3 advanced yolked oocyte (AYO), in which the oocyte is completely opaque except the perivitelline border; (**B**) late migratory nucleus-stage oocyte (MNO), in which some droplets of the peripheral yolk have coalesced and become translucent; and (**C**) hydrated oocyte (HO), in which the whole oocyte is translucent.

Table 3

Results of a stepwise multiple regression of the total fecundity of vermilion snapper on ovary-free weight and mean oocyte diameter for a succession of oocyte diameter classes. Dashed line separates oocyte diameter classes, where diameter is a significant variable, from those where it is not.

	Multiple regression coefficient and t-ratio						
	Constants		Fish weight		Oocyte diameter		
Oocyte diameter class (mm)	n	a	b_1	t	b_2	t	r^2
0.360–0.470	59	–271,217	83.5	2.73	720,838	5.86	0.405
0.365–0.470	58	–273,751	84.0	2.71	726,434	5.57	0.384
0.370–0.470	57	–274,239	84.1	2.66	727,502	5.24	0.357
0.375–0.470	55	–267,604	84.1	2.56	712,304	4.56	0.306
0.380–0.470	52	–228,103	87.9	2.54	620,040	3.34	0.230
0.385–0.470	50	–242,944	106	2.95	645,696	3.31	0.260
0.400–0.470	48	–239,170	112	3.04	634,478	2.98	0.248
0.405–0.470	47	–229,442	189.3	4.15	578,788	2.87	0.347
0.410–0.470	41	–247,829	210.5	4.47	611,076	2.55	0.385
0.415–0.470	40	–233,730	214.7	4.48	577,705	2.33	0.389
0.420–0.470	34	–295,305	222.9	5.24	711,614	2.86	0.506
0.425–0.470	27	–312,154	355.1	6.66	694,250	2.52	0.684
0.430–0.470	24	–300,087	364.1	6.45	663,948	2.09	0.680
0.435–0.470	18	–501,504	389.7	6.64	1,093,714	2.63	0.750
0.440–0.470	16	–510,147	398.6	6.74	1,108,996	2.40	0.782
0.445–0.470	13	–700,475	551.9	5.41	1,462,344	2.85	0.770
0.450–0.470	7	–652,740	536.4	2.37	1,365,795	.855	0.749

greater than 0.445 mm. Thus, only females with a MOD greater then 0.445 mm were used to estimate PF. Fecundity was regressed on OFWT to evaluate the predictability of the relationship.

Batch fecundity was determined by calculating the number of migratory nucleus-stage oocytes (MNO's; Fig 2B) or hydrated oocytes (HO's; Fig. 2C) in two weighed subsamples from each female (Hunter et al., 1992). Ovaries that contained hydrated oocytes loose in the lumen were eliminated from BF analyses. A modified version of the hydrated oocyte procedure of Hunter et al. (1985) was also used in BF estimates. Definitions from Hunter et al. (1992) were used to separate each spawning batch (Table 4). To see if batch size varied with the order of spawning, a one-way ANOVA was run on 49 females. To evaluate the temporal effects on BF, ANCOVA was run on monthly equations of BF.

Exact ages of POF's were not known because sampling on MARMAP cruises occurred only from dawn through dusk and because trap deployment time was assigned to the catch, regardless of when the fish entered the trap. Therefore, we defined POF's in terms of "new" and "old," on the basis of data from reports in the literature and from our observations. There is limited work on other lutjanids (Davis and West, 1993); thus, descriptions from Hunter and Macewicz (1985) were also used to define POF's. New POF's were generally large and had an orderly arrangement of distinct columnar granulosa cells with prominent nuclei intact (Fig. 3A). New POF's resembled the early stage POF of *Lutjanus vittus* (Davis and West, 1993). Old POF's were small, coiled, eosin-

Table 4

Batch number classification for vermilion snapper following Hunter et al. (1992).

Batch number	Definition
1	Nonhydrated advanced yolked oocytes (AYO's) present and post-ovulatory follicles (POF's) absent.
2	One class of POF's and nonhydrated AYO's present.
3	Two classes of POF's and nonhydrated AYO's present.
4	Only one batch of migratory nucleus-stage oocytes (MNO's) and one batch of hydrated oocytes (HO's) present, no other AYO's present.
5	Only one batch of HO's present, no other AYO's present.

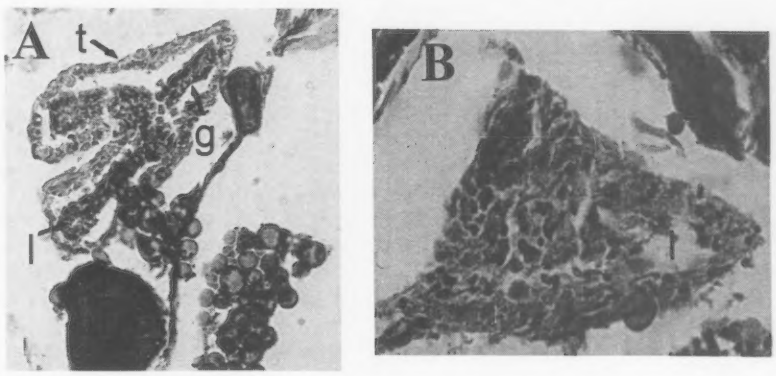

Figure 3

Photographs of histological section of the ovary of vermilion snapper, showing (**A**) new postovulatory follicle (POF) at 100×, in which the columnar granulosa cells with prominent nuclei are distinct and the lumen is visible, and (**B**) old POF at 400× with a typical triangular shape, in which most of the granulosa cells without nuclei are disintegrating. (g=granulosa layer, t=thecal layer, l=lumen)

y–stained structures with approximately half to very few of the granulosa cells intact (Fig. 3B). Old POF's resembled 1-day-old POF's of *Engraulis mordax* (Hunter and Macewicz, 1985). To confirm temporal trends in the occurrence of hydrated females, the samples collected for this study were supplemented with additional histological slides (from spawning females collected on MARMAP research cruises in 1991 and June to August 1993) for examination of POF age.

To calculate spawning frequency, the method of Fitzhugh et al. (1993) was used to calculate overall percentages of HO's, new POF's, and old POF's. A proportion was computed for each category by dividing the total number observed in each category by the total number of mature females. An overall average was computed by summing the three category proportions and by dividing by three. The overall average was then multiplied by number of days in the spawning season to determine spawning frequency. We defined the spawning season as the date (15 April 1992) when spawning condition was histologically evident until the date (24 September 1992) when major atresia of AYO's first occurred. If the proportions for each criterion were independent of those of other criteria and similarly distributed, then they could be combined to increase the sample size (Alheit et al., 1984). If spawning frequencies are to be combined, they must not be statistically different; therefore, we used the Mann-Whitney test to examine differences between frequencies of the HO's versus new POF's and between new POF's versus old POF's.

Results

Sex ratio, ovarian development, maturity, and spawning season

Vermilion snapper did not exhibit a 1:1 sex ratio; females were 63% of the samples (Table 5). Comparisons of sex ratio by 5-cm length classes revealed significant differences from a 1:1 ratio for every length class. Trap and hook-and-line samples collected during MARMAP cruises and samples collected by the commercial hook-and-line fishery yielded similar sex ratios. The sex ratio from Grimes (1976) was comparable to the sex ratio for all samples of vermilion snapper in this study.

Oocyte size-frequency (percent) distributions for five oocyte stages (Fig. 4) revealed the developmental sequence of ovary maturation. Oocyte size was correlated with stage of development; however, there was considerable overlap in size between stages. This asynchronous pattern of development means that the number of batches cannot be inferred from the size-frequency distribution of oocytes.

The mean oocyte diameter (MOD) appeared constant over the spawning season (Fig. 5). This is evidence that oocytes matured and were developing throughout the spawning season.

Table 5

A comparison of sex ratios among different groups of vermilion snapper.

Comparison group (and ratios)	χ^2	P	Result
Females vs. Males: (62.6% vs. 37.4%; 1.67:1)	6.35	$0.025<P<0.01$	Significant difference from 1:1 ratio.
MARMAP catches (67% female) vs. commercial catches (57% female)	1.72	$0.10<P<0.25$	No significant difference between the sex ratios of MARMAP catches and commercial catches.
Length-class comparison 20–24 cm TL: 62.7% female 25–29 cm TL: 66.5% female 30–34 cm TL: 64.3% female 35–39 cm TL: 68.1% female	9.92	0.0193	Significant difference from 1:1 ratio within each 5 cm length classes.
Grimes (1976) vs. present study (62.5% vs. 62.6% females, respectively)	0.01728	$0.75<P<0.90$	No significant difference between overall sex ratios of Grimes (1976) and the present study.

All vermilion snapper in this study were mature. Of the 750 females (Table 6) and 254 males (Table 7) examined histologically, the smallest female was 165 mm FL (186 mm TL) and smallest male 179 mm FL (197 mm TL). Ages of 176 females ranged from 2 to 10 yr; 87 males ranged from 3 to 11 yr (Tables 6 and 7).

Owing to gear selectivity, fish under two years old were not found in the present study; however, three- and four-year old fish were about the size of those found by Grimes (1976) (Fig. 6). After age four, fish in the present study were dramatically smaller than fish in the study by Grimes (1976).

The spawning season of vermilion snapper was from April to September (Fig. 7). The mean gonadosomatic index (GSI) for females increased in April and was high through August, decreasing in September. Mean GSI values remained constant from October through March. Spawning was first evident histologically on 15 April 1992 and no longer evident in sections taken at the end of September 1992. Gonad index (GI) values of Grimes (1976) for 1973–74 showed trends similar to those for GI values from this study (Fig. 8).

Reproductive activities of males began earlier in the year and lasted longer in the season than did the reproductive activity of females (Fig. 9). Percentages of active males and females were similar for July, August, and September. There were reproductively active portions of the population present from April through October (during which period there were correspondingly higher GSI values for females).

Table 6

Number of mature specimens by size class for 750 female vermilion snapper. Specimens with evidence of histological criteria I–V (see Hunter et al., 1992) were considered mature. All females were examined histologically.

	Age (yr)										
FL (mm)	2	3	4	5	6	7	8	9	10	11	No age
151–175											1
176–200	1	6	3	3	1	1					142
201–225	2	3	6	6	4	2	2				227
226–250	1	2	4	22	12	4	2				92
251–275		2	9	14	6	5	1	2			60
276–300	1		5	17	4	1					31
301–325			3	2	4	1	1	1			13
326–350			2	1	1	1					3
351–375				1		1	2		1		5
Total	5	13	32	66	32	16	8	3	1		574

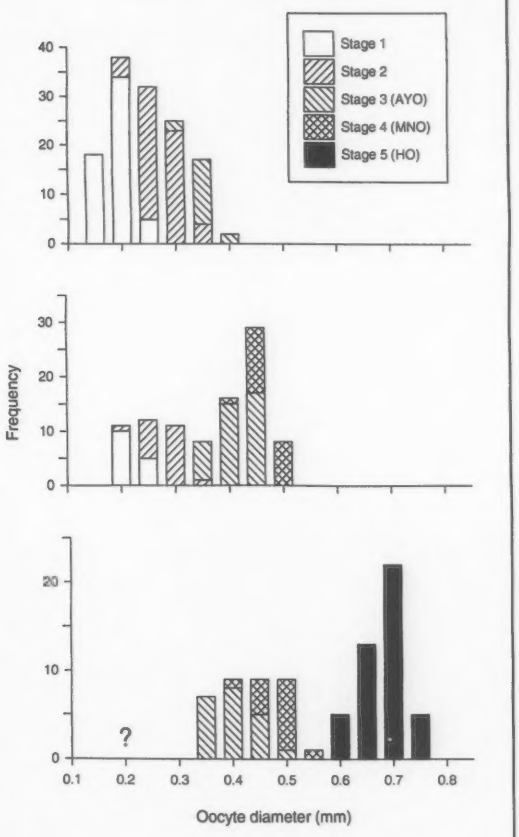

Figure 4

Oocyte size-frequency (percent) distributions and oocyte stage of three mature vermilion snapper representing the developmental sequence of maturation. Females were collected in May and length range was 192 mm to 213 mm FL. (? = stages that were not counted.)

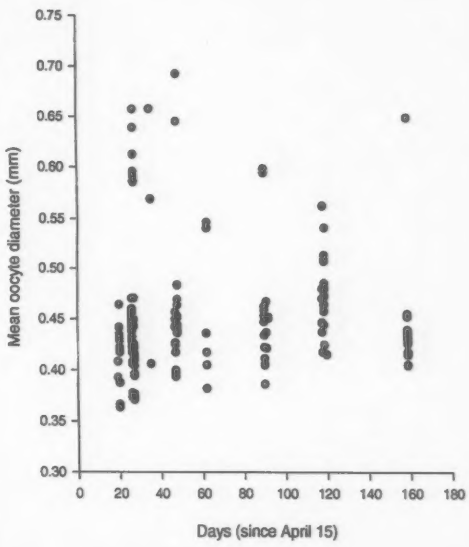

Figure 5

Mean oocyte diameter of vermilion snapper versus number of days since April 15.

Fecundity

Location of oocytes within the ovary revealed no significant effect on oocyte density (Table 8). Advanced yolked oocytes (AYO's) were randomly distributed within the ovary; samples could be taken from any location within the ovary without bias.

The relationship between ovary-free body weight (OFWT) and potential fecundity (PF) was expressed by the following equation:

$$PF = -25{,}992 + (508 \times OFWT).$$

The coefficient of determination (r^2) was 0.583 for the 13 fish used in the analysis (Fig. 10). The PF ranged from 17,374 to 122,130 oocytes for an OFWT range of 109 g to 265 g.

Monthly mean TF estimates of vermilion snapper increased from 54,100 oocytes in May (n=16, OFWT range 109–194 g) to 118,500 in August (n=25, OFWT range 108–442 g); then decreased to 58,200 in September (n=15, OFWT range 106–238 g). Analysis of covariance of monthly equations of TF on OFWT indicated that equations were similar over the spawning season (Fig. 11). The slopes of the equations were similar (F=0.02984, df=4,85, P>0.25) and, assuming a common slope, there was no significant difference in intercepts between months (F=0.02936, df=4,89, P>0.25). Regression of TF on OFWT for days elapsed since 15 April indicated that the coefficient for elapsed days was not significant (t=1.338, df=94, P=0.1842). Thus, TF did not decline continually over the spawning season.

In whole oocyte samples used to estimate fecundity, the average fraction of AYO's that were atretic was 0.011 (SD=± 0.023, n=138). Minor alpha atresia of AYO's was observed in 29% of the fish used in fecundity estimates. A stepwise multiple regression of OFWT, days, and atretic fraction of AYO's on TF, indicated that the coefficient for the atretic fraction of AYO's was not significant and thus atresia does not result in a significant loss of oocytes (Table 9).

Table 7

Number of mature specimens by size class for 254 male vermilion snapper. Males were classified as mature based on criteria in Table 2. All males were examined histologically.

	Age (yr)										
FL (mm)	2	3	4	5	6	7	8	9	10	11	No age
151–175											0
176–200			2	2							40
201–225				5	2	2	1				50
226–250		1	2		1	1					28
251–275		1	13	14	3	6	1	1	1		22
276–300			7	6	3	1					19
301–325			1	1	1						5
326–350			1	3	1					1	2
351–375				1	1						0
376–400											1
Total		2	26	32	12	10	2	1	1	1	167

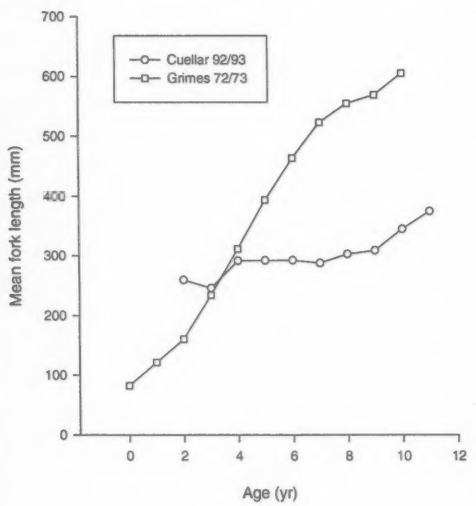

Figure 6

A comparison of mean fork length (at capture [in mm]) at age for vermilion snapper from 1972–73 (Grimes's study) with fork length at age from 1992 to 1993 (present study).

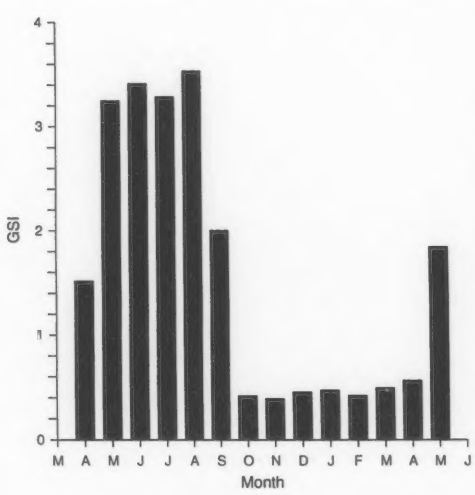

Figure 7

Gonadosomatic index (GSI) values by month for female vermilion snapper that were collected from April 1992 through May 1993. GSI = gonad weight (g)/ovary-free body weight (g).

Histological examination for alpha atresia of samples with AYO's (n=410) revealed that only 2% of all females had major alpha atresia of AYO's and that 27.5% had minor alpha atresia of AYO's (Table 10). Percentages of minor and major alpha atresia of AYO's were similar between whole oocyte samples and histological samples.

A one-way ANOVA on 49 females detected no significant difference among batch sizes (Table 11). All spawning batches were found throughout the spawning season, with batch 1 and batch 2 having the highest percentages in each month (Fig. 12). The relationship between fish length and batch fecundity was best described by the following equation, with r^2= 0.444 (Fig. 13):

Table 8

Effect of location of tissue samples within the ovary on oocyte density (number of advanced oocytes per unit sample weight) vermilion snapper for mean, standard deviation (SD), and two-way analysis of variance of results are given.

	Location of sample			Oocyte density	
Position no.	Lobe	Long. plane	*n*	Mean	SD
1	Left	Anterior	9	4470.7	3311.8
2	Left	Center	9	5730.9	4721.0
3	Left	Posterior	9	4660.6	3266.1
4	Right	Anterior	9	3619.7	2112.3
5	Right	Center	9	5746.9	2629.3
6	Right	Posterior	9	4633.3	2501.3

	Analysis of variance on six locations within the ovary of vermilion snapper				
Source	df	Sum of squares	Mean square	*F*	*P*
Fish	8	150,536,374.2	18,817,046.8	2.007	0.0704
Location	5	29,043,522.9	5,808,704.6	0.620	0.6855
Error	40	374,972,921.2	9,374,323.0		
Total	53	554,552,818.3	10,463,260.7		

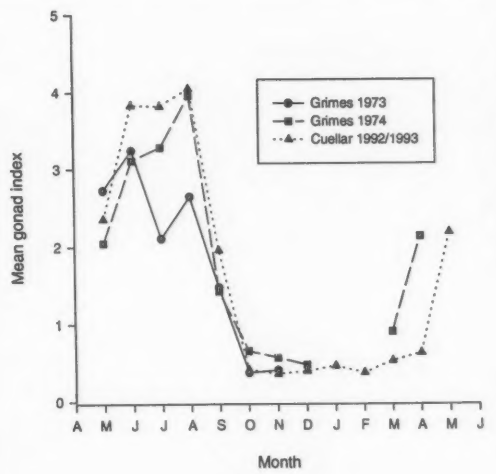

Figure 8

A comparison of mean gonad index [$K_G=(WT_G/TL^3)\times 10^6$] by month for vermilion snapper from 1973 and 1974 (Grimes, 1976) with mean gonad index by month in the present study (1992–93).

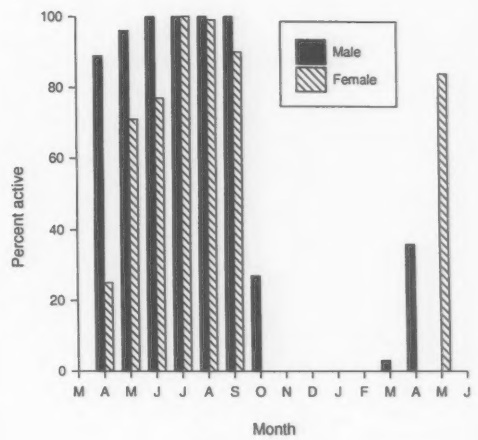

Figure 9

Percentages of reproductively active male and female vermilion snapper in each month from April 1992 through May 1993.

$BF = 0.0438FL^{2.508}$ (F=37.6, df=1,47, P <0.0001);

and the relation between OFWT and batch fecundity by the following equation, with r^2 = 0.332 (Fig. 14):

$BF = 14{,}037 + (112 \times OFWT)$ (F=23.3, df=1,47, P<0.0001).

Batch fecundity varied remarkably among fish of the same size (Table 12; Fig. 13). ANCOVA was run on monthly linear regression equations of FL on BF.

This analysis indicated that the slopes were similar between months (F=0.06548, df=4,44, P>0.25). Assuming a common slope, we concluded that there were no differences among intercepts of each month (F=1.90, df=4,44, 0.10<P<0.25). The variation of BF estimates was high (4,000–90,000 oocytes), and there was not a significant difference in BF between months.

Spawning frequency

Although no significant temporal trends in the frequencies of POF's were evident, the following observations provide a preliminary age to new POF's of vermilion snapper. MARMAP sampling occurred

Table 9

Analysis of the relation between total fecundity on ovary-free body weight (OFWT), on elapsed days since April 15, and on fraction of atretic oocytes of vermilion snapper with stepwise regression. Boldface refers to the coefficient of the atretic fraction of oocytes.

	Step		
	1	2	3
Constant	26,848.2	–6,968.8	–9,117.2
OFWT	258.8	291.7	293.7
t	6.398	7.620	7.597
P			<0.0001
Days		403.1	415.9
t		4.703	4.589
P			<0.0001
Atretic oocytes			81177.8
t			**0.445**
P			0.6574
r^2	0.2313	0.3395	0.3405
Adjusted r^2	0.2257	0.3298	0.3258

Table 10

Histological determination of number of vermilion snapper with no atresia, minor atresia (<49%), and major atresia (>50%) of advanced yolked oocytes (AYO's) expressed as a percentage of all females with AYO's during the spawning season (April–October).

State	Atresia	Percentage	Number
Nonspawning	none	41.4	172
Nonspawning	minor	22.4	93
Spawning	none	28.2	117
Spawning	minor	5.1	21
Inactive	major	2.2	9
Total			415
Total samples without AYO's			335
Total: minor		27.5	114
Total: major		2.2	9

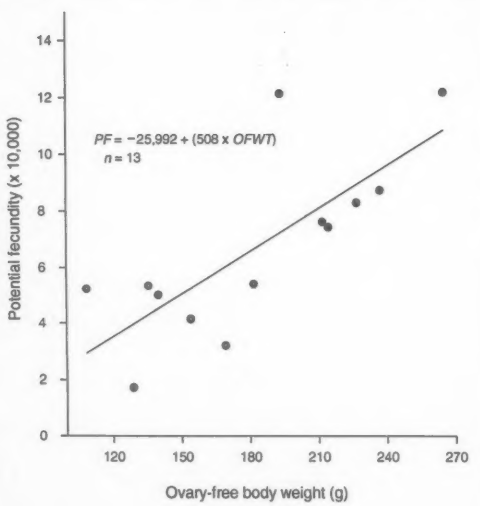

Figure 10

Linear regression of potential fecundity (PF) of vermilion snapper on ovary-free body weight (OFWT).

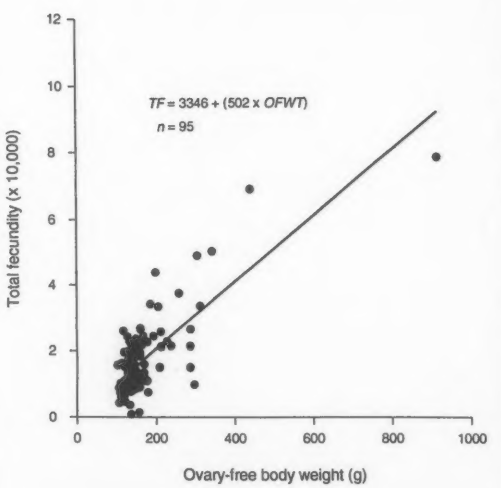

Figure 11

Linear regression of total fecundity (TF) of vermilion snapper on ovary-free weight (OFWT) in g.

from approximately 0800 to 1900 h local (Eastern) time and in all fish examined from samples collected during MARMAP cruises from 1991 to 1993, 70–100% of spawning females (i.e. those with hydrated oocytes (HO's); n=54) were captured between 1300–1900 h. During the April 1992–May 1993 sampling,

Table 11

Mean relative batch fecundity for five batch order numbers. Relative batch fecundity = number of oocytes/ovary-free body weight.

Batch number	No. of females	Relative batch fecundity Mean	SD
1	14	202	125
2	14	174	73
3	2	271	34
4	16	193	59
5	3	186	111

ANOVA on five batch orders

Source	df	Sum of squares	Mean square	F	P
Batch order	4	34,753.7	8,688.4	1.331	0.282
Error	44	189,321.1	6,528.3		
Total	48	367,605.5	7,658.4		

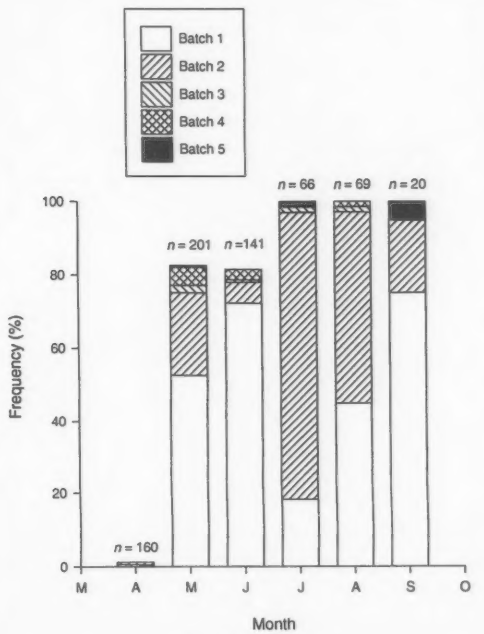

Figure 12

Percent frequencies of batch numbers by month for vermilion snapper. Definitions for batch numbers are listed in Table 4. n = total number of females collected each month.

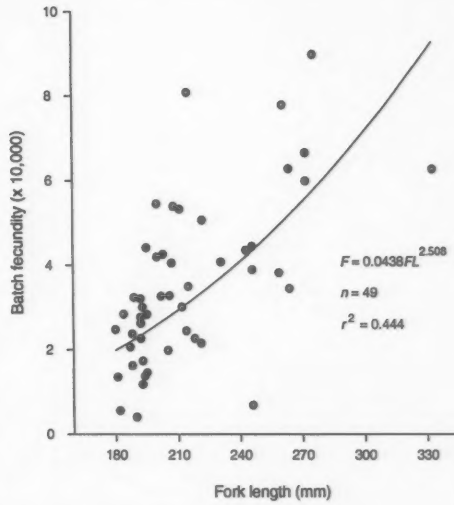

Figure 13

Nonlinear regression of batch fecundity (BF) of vermilion snapper on fork length (FL) in mm.

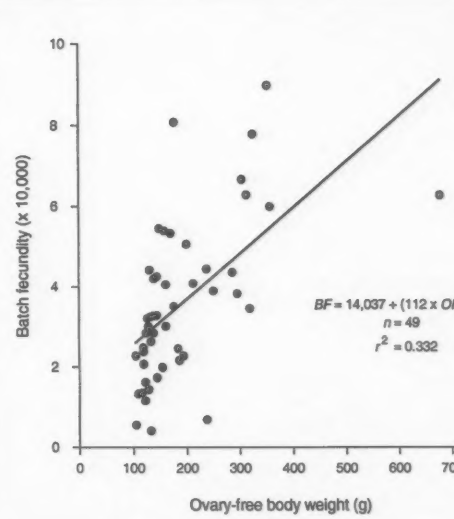

Figure 14

Linear regression of batch fecundity (BF) of vermilion snapper on ovary-free weight (OFWT) in g.

80% of hydrated females (n=10) were found between 1300–1800 h. In 1992, 70% of fish with new POF's (n=25) were collected between 0800–1200 h. Histological examination of 128 females (from April 1992 to May 1993 [MARMAP sampling]) revealed that only two fish had hydrated oocytes (HO's) as well as old POF's and that only seven fish had two classes of POF's (new and old). Because new POF's in lutjanids are ~12–24 hours old (Davis and West, 1993), these new POF's in vermilion snapper indicate that spawning took place during the previous afternoon or evening.

In 23 collections, 3.5% of spawning females had HO's, 8.9% had new POF's, and 30.5% had old POF's (Table 13). This finding corresponded to a spawning periodicity of about every seven days or 23 times per

Table 12

Fork length (FL), ovary-free body weight (OFWT), batch fecundity (BF), and annual fecundity (AF) ranges by month for vermilion snapper from the southeastern United States. Annual fecundity is the batch fecundity multiplied by the spawning frequency (35 times). n = number of specimens.

Month	n	FL range (mm)	OFWT range (g)	BF range (no. of oocytes)	AF range (no. of oocytes)
May	17	180-333	109–678	4,005–90,000	140,175–3,150,000
Jun	11	187–259	119–296	16,312–54,519	570,920–1,908,165
Jul	9	182–211	105–170	5,520–53,972	193,200–1,889,020
Aug	9	195–264	124–313	28,289–80,848	990,115–2,829,680
Sep	3	188–246	119–238	6,846–23,685	239,610–828,975

Table 13

Numbers of female vermilion snapper with histological evidence of spawning used to determine spawning frequency. Hydrated oocytes (HO's), new postovulatory follicles (POF's), and old POF's were classified according to descriptions from Hunter and Macewicz (1985) and Davis and West (1993) (See Fig. 3, A and B). Sampling period in 1992 was 162 days. Total % was calculated by dividing the total of each category by the total number of mature females (282) and by multiplying by 100.

Date	Collection	No. of HO's	No. of new POF's	No. of old POF's	Total mature
15 Apr	1077			1	1
4 May	1129–1133			1	8
20 May	1169–1173	2	4		8
1 Jun	1175–1180			4	37
2 Jun	1183–1188	1	1	3	33
2 Jun	1203	1			7
16 Jun	1241			1	25
16 Jun	1246–1248	2			8
14 Jul	1312–1317		6	1	13
14 Jul	1319–1323			5	6
14 Jul	1331–1333	2		1	4
15 Jul	1336–1340		4		5
15 Jul	1342–1347		4		4
15 Jul	1351–1352			3	5
16 Jul	1355–1358		1	10	12
16 Jul	1362–1364		1	18	19
11 Aug	1371			1	1
11 Aug	1373			1	1
11 Aug	1378–1384	1		7	13
12 Aug	1388–1390			11	22
12 Aug	1395			12	24
13 Aug	1408–1410			6	6
21 Sep		1	4		20
Total		10	25	86	282
Total %		3.50	8.90	30.50	

year. From visual observations of histological slides, it appeared that the duration of HO's and new POF's might be more similar than the duration of new POF's and old POF's. Thus, we decided to test the populations statistically to see if this might be true. There was no difference in the frequencies of HO's and new POF's (Mann-Whitney, n=23, P=0.675), but there was a significant difference in the frequencies of new POF's and old POF's (Mann-Whitney, n=23, P= 0.00598). Thus, HO's and new POF's probably have similar durations that allow us to combine the categories statistically to increase the sample size. An overall average was recalculated by summing only two categories ((*HO+new POF*)/2, and *old POF*) and by dividing by two. This overall average was then multiplied by days in the spawning season to determine a new spawning frequency. Combining categories results in a spawning frequency of approximately every five days or 35 times per year. The duration between new POF's and old POF's was long enough that the combination of categories was not statistically possible.

Discussion

Hunter et al. (1992) listed four lines of evidence that indicate determinate fecundity (see Materials and Methods section). Vermilion snapper, however, is an indeterminate spawner because it does not demonstrate any of the four characteristics given for determinate fecundity. Each line of evidence is addressed in detail in the following section.

The oocyte size-frequency distribution is continuous in vermilion snapper (without a hiatus between any oocyte stages) except for the hydrated batch. Traditional evidence for determinate fecundity is 1) the obvious gap in oocyte maturity stages or size classes among the oocytes that are maturing during the season and 2) the reservoir of less mature oocytes present year-round in the ovary (Yamamoto, 1956). Although the absence of such a hiatus is evidence for indeterminate fecundity, in some cases fish with a continuous oocyte distribution are still considered to have determinate fecundity (Hunter and Macewicz, 1985). In such cases, the product of batch fecundity multiplied by spawning frequency needs to be compared with the standing stock of mature oocytes at the beginning of the season. For example, a 300-g vermilion snapper in this study produces approximately 126,408 oocytes on the basis of the potential fecundity equation, whereas a 300-g female produces approximately 1.7 million oocytes according to the product of BF multiplied by spawning frequency. It is quite obvious from this study that the product of BF multiplied by spawning frequency must be used to estimate annual fecundity.

The mean oocyte diameter of vermilion snapper stayed constant over the spawning season. Species with determinate fecundity would produce larger oocytes as the season progressed because, as maturation continued during the spawning season, no new oocytes would be recruited into the advanced stock, and eggs that were present would be developing and increasing in size. In contrast, indeterminate spawners are continually producing oocytes during the spawning season, with smaller immature oocytes replacing those that mature and are spawned, resulting in a constant MOD.

Total fecundity and BF in vermilion snapper did not consistently decline over the spawning season as would be expected if the vermilion snapper was a determinate spawner. Total fecundity and BF actually increased through August and declined in September in this study. No trends in TF existed over the months of the spawning season. Atresia also had no significant effect on fecundity estimates to account for a decrease in the number of oocytes. Similarly, Davis and West (1993) found that the BF of *Lutjanus vittus* did not decline over the spawning season. Vermilion snapper in the northern central Gulf of Mexico appear to have a similar trend of peak spawning in late summer according to larval abundances found in that area (Comyns and Lyczkowski-Shultz[3]). Grimes (1976) found peak spawning activity (according to gonsomatic index [GSI] values) in August off the Carolinas, and Nelson (1988) found peak activity in the Gulf during the summer. This trend toward peak spawning during middle to late summer would be expected for an indeterminate spawner with continuous development of oocytes over the reproductive season.

The order of spawning batches was not consistent with the determinate fecundity prediction. Of 750 females examined histologically, three had hydrated oocytes (HO's) in the ovary in the absence of any other advanced-stage yolked oocyte (AYO) batch, and only 16 had a batch of early migratory nucleus-stage oocytes (MNO's) and a late HO batch. Many of the females sampled from September contained all mature oocyte stages, except in the HO batch.

According to Hunter and Macewicz (1985), determinate fecundity is generally found in species in cooler climates and with shorter spawning seasons. Many fishes (snappers, grunts, jacks, dolphin, some

[3] Comyns, B. H., and J. Lyczkowski-Schultz. 1993. Spawning and early life history of snappers in the northcentral Gulf of Mexico. Proceedings of the sixth annual MARFIN conference; Atlanta, Georgia, 12–13 October 1993, p. 1–3.

porgies, and sea basses) in the Carolinas have a protracted spawning season extending from early spring to early fall (Hardy, 1978; Johnson, 1978; Grimes, 1987). The southeastern United States has temperate and tropical characteristics, with surface water temperatures from about 22°C to 29°C (Mathews and Pashuk, 1986) and bottom temperatures of 15°C to 25°C on the middle continental shelf (18–60 m) during summer (present study). Vermilion snapper fit the expectation of being indeterminate spawners on the basis of the temperate and tropical characteristics of this area and on the basis of their long spawning season.

Length was the best predictor of batch fecundity, but great variability was seen in BF estimates for same-size fish, perhaps because some oocytes may have been spawned. This is not likely, however, because fish with hydrated oocytes free in the lumen and fish with postovulatory follicles (POF's) were not used in BF estimates. The monthly average BF appeared to peak in August and decline in September. However, time (months) did not have a significant effect on BF estimates, and it is unlikely that differences in station locations within the sampling area could account for the variation in BF. Davis and West (1993) suggested that the variation seen in BF estimates of *Lutjanus vittus* might be due to the collection of samples during various phases of the lunar cycle. *Lutjanus vittus* seemed to follow a lunar rhythm in spawning, as do many lutjanids (Grimes, 1987; Carter and Perrine, 1994). Thresher (1984) suggested that lunar periodicities are probably universal in lutjanids. Environmental cues of spawning events were not examined in this study; however, Grimes (1976) found that vermilion snapper spawning correlated with temperature and photoperiod, but not with the lunar cycle.

Because of differences in fecundity estimation methods, comparisons between the present study and that of Grimes (1976), or with most other studies on lutjanids, are not particularly useful (Grimes, 1987). For example, Grimes (1976) estimated fecundity on vermilion snapper taken off the Carolinas early in the season. He counted all developing oocytes in each female (the total count is approximately equivalent to a PF estimate in this study). His fecundity equation for a 300-g fish results in a fecundity estimate of 49,152 oocytes, compared with a PF of 126,408 oocytes for the same size fish in the present study.

Collins and Johnson[4] used the hydrated oocyte method (Hunter et al., 1985; Hunter and Macewicz, 1985) for spawning frequency and annual fecundity measurements of vermilion snapper in the northeastern Gulf of Mexico. The spawning frequency (44 times per year) of vermilion snapper in the Gulf exceeded spawning frequency in this study (35 times per year). Also, the annual fecundity of the vermilion snapper in the Gulf (1.32 to 21.9 million eggs) was much higher than the annual fecundity determined in the present study for vermilion snapper in Atlantic waters off the southeastern United States (140,175 to 3.2 million eggs). The spawning season of vermilion snapper in the Gulf is slightly longer than the spawning season of vermilion snapper in the southeastern United States (April to late September), and this additional time in the warmer waters of the Gulf may result in the differences in annual fecundity estimates between the two regions. The use of the hydrated oocyte method instead of the postovulatory method to estimate spawning frequency may also account for the difference between the two studies.

Larger fish in the Gulf study may also account for some of the differences in annual fecundity estimates between the two studies; however, the sizes of fish studied by Collins and Johnson[4] were not available. The largest female in the present study was 440 mm TL, but the majority of the vermilion snapper were between 200 mm TL and 300 mm TL. It is generally accepted that larger females produce more oocytes. Grimes and Huntsman (1980) found that fecundity increased dramatically in larger (older) vermilion snapper.

Davis and West (1993), using new assessment techniques, found that the annual fecundity of a 300-mm *Lutjanus vittus* was about 4.5 million oocytes (if it spawned 90 times a season) or 7.6 million oocytes (if it spawned 150 times a season) on the northwest shelf of Australia. This annual fecundity estimate for *Lutjanus vittus* is closer to the annual fecundity estimate for vermilion snapper (140,175 to 3.2 million eggs) in this study than to the estimate for vermilion snapper calculated by Collins and Johnson.[4] Examination of the annual fecundity estimates reveals that the major difference between vermilion snapper and *Lutjanus vittus* is spawning frequency. Batch sizes were relatively similar: a batch size for a 300-mm *L. vittus* was about 71,000 oocytes and a batch size for a similarly sized vermilion snapper was about 50,000 oocytes. The spawning season for *Lutjanus vittus* is year round, and most spawning occurs from September to April. The longer spawning season of *L. vittus* accounts for a major portion of the large difference in spawning frequency between the two species.

In the vermilion snapper of our study, POF's could not be given an exact age because of a lack of 24-h sampling and because of small sample sizes; therefore time of day for spawning could not be deter-

[4] Collins, L. A., and A. G. Johnson. 1994. Spawning and annual fecundity of gag, red snapper and vermilion snapper in the northeastern Gulf of Mexico. Southeastern U.S. and Caribbean reef fish workshop: Charleston, South Carolina, 15–16 September 1994 [abstract].

mined. Because of these limitations the spawning-frequency estimate calculated in this study should be considered preliminary. More detailed work needs to be done to calculate a more representative spawning-frequency estimate for the population in this region. Additional work should include sampling over a 24-h period for a series of days during the spawning season to define POF age from a larger number of fish.

In spite of limitations, a preliminary estimate of spawning time and POF duration can be derived from the literature and our observations. Postovulatory follicles in *Lutjanus vittus* persist for only about 24 h (Davis and West, 1993), and POF's in vermilion snapper may be similar in duration owing to the higher temperature of shelf waters during the spawning season, which may accelerate reabsorption of POF's (Hunter and Macewicz, 1985). Most lutjanids appeared to spawn at dusk (Wicklund, 1969; Starck and Schroeder, 1971; Thresher, 1984) but recently some lutjanids were found to spawn in the mid-afternoon (Davis and West, 1993; Carter and Perrine, 1994). In addition, vermilion snapper are nocturnally active (Grimes, 1979; Sedberry and Cuellar, 1993); thus spawning activity may continue into the night. In the present study, some vermilion snapper appeared to spawn from mid-afternoon to early dusk, as do other lutjanids; when the majority spawn was not determined.

A comparison of the sex ratio, based on present data and Grimes (1976), indicated that the sex ratio of vermilion snapper had not changed in 20 years (62.6 and 62.5% females, respectively). Sex ratios for western Atlantic snappers often deviate from 1:1, with males outnumbering females in more cases than the reverse (Grimes, 1987). MARMAP data collected with standardized methods over a 15-yr period revealed an increase in the percentage of females in the vermilion snapper population in the region from about 60% in 1978–79 to about 72% in 1991–93 (Zhao and McGovern[1]). This change in sex ratio has occurred in spite of no significant difference in fishing mortality (F) between males and females (Zhao and McGovern[1]). Temperature changes have been known to induce change in sex ratio in fish (Lagomarsino and Conover, 1993) but summer water temperatures on the middle and outer continental shelf off the southeastern United States have been remarkably uniform for the 17 years preceding this study (National Environmental Satellite, Data, and Information Service[5]). Decreases in mean size of vermilion snapper in recent years are well documented (Collins and Sedberry, 1991; Zhao and McGovern[1]). This change in size may be caused by intense fishing, which is believed to have resulted in fewer individuals and smaller fish size (Collins and Pinckney, 1988; Bas and Calderon-Aguilera, 1989; Sutherland, 1990) and, hence, reduced fecundity (PDT, 1990). Unknown compensatory mechanisms may be at work under the intense selection pressure exerted by fishing on vermilion snapper; these mechanisms may result in altered sex ratios to compensate for reduced individual fecundity.

All vermilion snapper in this study were mature, with the smallest fish measuring 186 mm total length (TL). The smallest aged fish was two years old at 186 mm TL. Grimes (1976) found most mature fish at age three were 186–256 mm TL and at age four were 256–324 mm TL; only a few individuals matured in their second year at approximately 150 mm TL. After age four, vermilion snapper in our study were much smaller than those in the study by Grimes (1976). The size difference could, again, be explained by increased fishing pressure or by the fact that Grimes (1976) used scales and whole otoliths, not sectioned otoliths, to determine age. Collins and Pinckney (1988), like Grimes (1976), used scales rather then sectioned otoliths and found that 60% of females and 90% of males mature at 160 mm TL. Recently, Zhao and McGovern[1] found mature vermilion snapper at an even a smaller size, with 100% of males and females mature at 140 mm TL. This change in size at maturity may be a result of fishing pressure.

Vermilion snapper has a protracted spawning season throughout the summer months in the southeastern United States. The gonad index used by Grimes (1976) indicated that vermilion snapper in this area spawn from late April to September. In the Carolinas and Georgia, Powles (1977) and Fahay (1975) found high abundances of larvae during July–September, although they did not sample beyond that period of time. Nelson (1988) and Collins and Johnson[4] found that the spawning season of vermilion snapper occurred during spring and summer in the Gulf of Mexico. Also in the Gulf of Mexico, Comyns and Lyczkowski-Shultz[3] indicated that spawning occurred from May through September on the basis of abundance of larvae. However, in Puerto Rico, Boardman and Weiler (1979) found that vermilion snapper spawned year round, and Munro et al. (1973) found a ripe female vermilion snapper in November in Jamaica. Restricted spawning and year-round spawning in the same species may reflect a difference between temperate and tropical locations, or as Grimes (1987) suggested, a difference between con-

[5] National Environmental Satellite, Data, and Information Service. 1992. Oceanographic monthly summary, July 1978–July 1992. U.S. Dep. Commer., National Ocean Service, National Weather Service. Ocean Products Division, Camp Springs, MD.

tinental versus insular populations of snappers. Vermilion snapper in this study had a spawning season similar to many other continental populations of snappers as reviewed by Grimes (1987).

Grimes (1987) suggested that restricted spawning in continental species may be linked to the production cycle of the environment. Off the southeastern United States, upwelling occurs year-round, but it increases dramatically in spring and summer as the Gulf Stream moves farther offshore, allowing deep waters to upwell near the shelf break (Atkinson et al., 1985; Mathews and Pashuk, 1986). Topographic features in this area (i.e. the Charleston Bump) also cause upwelling events that bring nutrient-rich bottom water to the shelf areas (Mathews and Pashuk, 1986). Periodic meanders and eddies from the Gulf Stream add to the mechanism in which productivity of the shelf increases over the summer months. Phytoplankton blooms develop rapidly within the surface nutrient-rich water (Atkinson et al., 1984), thereby providing a large food source for larval and juvenile fishes. Spawning during this time of high productivity maximizes the survival of the larvae and juveniles of many of the reef fishes of the southeastern United States.

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Post-smolt growth, maturation, and survival of two stocks of Atlantic salmon

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Abstract.—Marine survival and sea-age at maturity of two hatchery-dependent stocks of Atlantic salmon were compared in respect to differences in post-smolt growth as evidenced by the circuli spacing patterns of their scales. The two stocks, the Penobscot and Connecticut, are located at the southern extent of the range of Atlantic salmon in North America. Return rates for 1SW (one seawinter) and 2SW salmon and the fraction of the smolt year class or cohort that matured as 1SW fish were found to be significantly higher for the Penobscot stock. Using image processing techniques, we extracted intercirculi distances from scales of 2,302 2SW fish. Circuli spacing data were expressed as growth indices for spring (when post-smolts first enter the ocean), summer (when growth appears maximal), and winter (when growth appears to be at a minimum). Circuli spacings of the Penobscot fish were wider during the summer season than were those for conspecifics from the Connecticut River of the same smolt year class. The results suggest that post-smolt growth may play a significant role in deciding age at maturity and survival patterns for Atlantic salmon stocks.

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Variation in the marine survival and sea-age of maturation of individual Atlantic salmon stocks, *Salmo salar* L., has ramifications for the management of these stocks in both freshwater and marine environments. Mixed-stock fisheries for salmon indiscriminately harvest stocks of varying productivity, often leading to the over harvesting of weaker stocks even when exploitation is at a level considered safe for the stock complex (Ricker, 1958). Homewater or terminal fisheries can also over harvest weak stocks when shifts in age at maturity and survival occur (Minard and Meacham, 1987). Understanding these periods of changing stock dynamics will help to ensure that management measures are taken to protect the stocks and enhance the fishery.

Events during the post-smolt year are critical to the survival and maturation of Atlantic salmon (Mills, 1989; Salminen et al., 1995); however, the factors shaping salmon population abundances during this period are poorly known (Friedland et al., 1993). Many sources of mortality, such as predation, disease, and parasitism, affect young salmon during their first year at sea. The effect of these sources of mortality is to some extent influenced by the size and condition of the post-smolts; thus, their effect would be expected to vary between years and among stocks (Mathews and Ishida, 1989; Holtby et al. 1990; Salminen et al., 1995). For example, predation during the post-smolt year may determine overall survivorship in salmon, but it is not known how much of the predation on young salmon is controlled by predator abundance versus the size and growth of the post-smolts themselves (Hislop and Shelton, 1993; Hargreaves, 1994). Predation theory suggests that the probability of survival for an individual increases considerably as its body size exceeds sizes vulnerable to potential predators (Werner and Hall, 1974; Mikheev, 1984; L'Abee-Lund et al., 1993). If juveniles remain in a developmental stage that makes them vulnerable to mortality, cumulative mortality will increase (Cushing, 1975). If a stock experiences depressed post-smolt growth, it may be susceptible to high mortality for a longer time compared with other stocks exploiting the same feeding area. Likewise, similar growth-mediated mechanisms can be envisioned for other sources of mortality such as diseases and parasitism.

The onset of sexual maturation in fishes is an inherited trait that operates within a range of phenotypic

plasticity (Via and Lande, 1985; Saunders, 1986; Stearns, 1992; Scheiner 1993; Trippel, 1995). Growth and environment during the post-smolt period play an important role in influencing the sea-age at maturation of salmon (Scarnecchia, 1983; Martin and Mitchell, 1985; Neilson and Geen, 1986; L'Abee-Lund, 1989; Scarnecchia et al., 1989; Skilbrei, 1989). Friedland and Haas (1996) found that summer post-smolt growth was positively correlated with maturation, suggesting that physical readiness to mature may be achieved during the summer period. Examining post-smolt growth in stocks with differing maturation rates should provide new insights into the mechanisms controlling salmon maturation.

In this study, we compare the marine survival and age at maturity of two hatchery dependent stocks of Atlantic salmon. We also describe and analyze circuli spacing and other length measurements from the scales of two seawinter returns to characterize growth during the post-smolt phase and to examine the role of post-smolt growth in affecting survival and maturation.

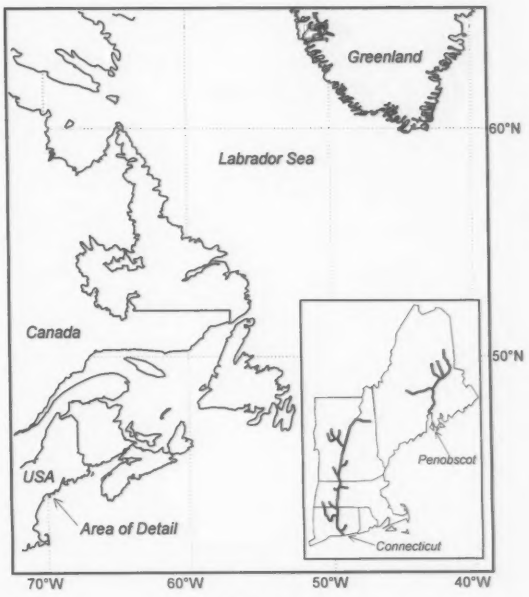

Figure 1

Map of the northwest Atlantic Ocean with detail showing location of the Penobscot and Connecticut rivers.

Materials and methods

Return rate and cohort age at maturity

Return rate by individual sea-age and cohort sea-age at maturity were calculated for two Atlantic salmon stocks, the hatchery components of the salmon runs in the Penobscot and Connecticut rivers in the United States. These rivers are situated at the southern end of the range of Atlantic salmon in North America (Fig. 1). Salmon from these rivers migrate to feeding areas as distant as the Labrador Sea. We analyzed data from 1977 to 1990, a period during which smolt releases in the Penobscot River ranged from 200,000 to 687,000 fish per year and in the Connecticut River from 32,000 to 476,000 fish per year (Table 1). Early in the time series, releases in both rivers were mostly two-year-old smolts, whereas in recent years, most of the releases have been yearlings. Freshwater returns of both 1SW (one seawinter) and 2SW salmon were ascertained from fishway trap counts and from recreational catches in the Penobscot River, as well as from trap counts in the Connecticut River (no legal Atlantic salmon fishery exists for this river). Return rates were calculated as simple ratios, expressed as returns per 1,000 smolts released.

The fraction of a cohort or smolt year class that matured after only a single winter at sea was derived by using both counts of adult returns by sea-age and fishing mortality that impacted the cohort. Fish from the Penobscot and Connecticut rivers were exploited in marine fisheries in Canada and Greenland during the study period. To account for this, we applied annual instantaneous fishing mortality rates (F in Table 1) for North American fish that were maturing as 2SW salmon (Friedland and Haas, 1996).

The observed return of 1SW salmon to freshwater (R_1) is the product of the maturation fraction (Ψ) and the size of the cohort immediately before the 1SW fish return to homewaters and the 1SW fisheries have commenced (N_0). Because we were modeling the cohort split immediately before the 1SW runs occur, natural mortality for this fraction of the cohort (M_1) was zero.

$$R_1 = N_0 * \Psi * \exp^{-M_1}. \quad (1)$$

The observed return of 2SW salmon (R_2) is assumed to be the remainder of the cohort that did not mature as 1SW fish and that survived for an additional 10 months at sea, plus the mortality associated with fishing (M_2=0.1 is from Friedland and Haas, 1996, and F is given in Table 1). The additional time 2SW salmon stay at sea is assumed to be 10 months, as opposed to one year, because 2SW salmon usually return to the river earlier in the year than 1SW fish.

Table 1

Smolt releases (number), returns (number), return rates by sea-age (‰), and 1SW fraction (Ψ) for the Penobscot (Pen) and Connecticut (Conn) Atlantic salmon stocks.

Smolt year	Smolt release		Yearling smolts %		1SW returns				2SW returns				Fishing mortality	1SW fraction	
					Pen		Conn		Pen		Conn				
	Pen	Conn	Pen	Conn	Return	Rate	Return	Rate	Return	Rate	Return	Rate		Pen	Conn
1977	388,500	96,400	34	0	123	0.36	3	0.03	671	1.98	50	0.52	0.511	0.091	0.032
1978	202,500	32,100	30	0	203	1.00	4	0.12	2,570	12.69	164	5.11	0.356	0.048	0.015
1979	296,300	124,900	17	0	652	2.20	4	0.03	2,454	8.28	513	4.11	0.433	0.135	0.005
1980	584,600	51,800	63	0	888	1.52	6	0.12	3,886	6.65	57	1.10	0.576	0.104	0.051
1981	199,500	78,600	12	7	155	0.78	3	0.04	705	3.53	39	0.50	0.592	0.099	0.037
1982	329,700	209,900	33	13	179	0.54	0	0.00	1,387	4.21	65	0.31	0.239	0.084	0.000
1983	436,700	98,000	63	91	239	0.55	7	0.07	2,868	6.57	293	2.99	0.218	0.057	0.017
1984	617,100	312,300	78	100	244	0.40	0	0.00	3,620	5.87	275	0.88	0.413	0.039	0.000
1985	580,900	255,000	82	100	534	0.92	0	0.00	1,477	2.54	343	1.35	0.490	0.167	0.000
1986	589,200	276,100	88	100	749	1.27	0	0.00	1,993	3.38	93	0.34	0.605	0.157	0.000
1987	539,200	205,800	85	100	716	1.33	1	0.00	2,005	3.72	58	0.28	0.480	0.167	0.010
1988	687,000	395,300	87	100	867	1.26	1	0.00	2,520	3.67	226	0.57	0.336	0.182	0.003
1989	416,600	217,700	84	100	430	1.03	1	0.00	1,085	2.60	168	0.77	0.428	0.189	0.003
1990	429,100	475,900	96	100	176	0.41	0	0.00	1,174	2.74	353	0.74	0.585	0.070	0.000
Mean			61	58		0.97		0.03		4.89		1.40		0.113	0.012

$$R_2 = N_0 * (1-\Psi) * \exp^{-(M_2+F)} \qquad (2)$$

Both equations contain N_0 and thus can be simplified to the expression

$$\Psi = \frac{\Phi}{(\Phi+1)}\ , \qquad (3)$$

where

$$\Phi = \frac{R_1 \exp^{-(M_2+F)}}{R_2 \exp^{-M_1}}\ . \qquad (4)$$

This formulation assumes that all individuals mature as either 1SW or 2SW fish. This is reasonable because returns of 3SW and older fish have been insignificant during the study period (typically less than 1% of the total runs).

The 1SW:2SW ratio has frequently been used as an index of 1SW maturation rate. However, sea-age classes are often affected by different patterns of marine mortality, particularly fishing mortality. Thus, the 1SW:2SW ratio is a satisfactory measure of maturation rate in only those instances where fishing mortality is constant over time and in fact is linearly related to 1SW maturation rate under these conditions. We know of considerable contrast in the fishing mortality time series for North American 2SW stocks, thus Ψ must be calculated.

Smolt size and age

The size of smolts as a factor affecting return rate and sea-age of maturation could not be directly evaluated in this study because smolt sizes were not available. However, comparability of the smolt releases in the two river systems and the transition from smolt releases of predominantly two-year-old fish to releases of yearling smolts raised concerns about the role smolt size may have had on the observed pattern of return rate and maturation. To address this concern, for each scale the length (mm) of the freshwater zone (taken as the distance from the focus to the end of the freshwater zone along the 360° axis of the scale) was measured (Fig. 2). Back-calculated lengths were not computed because of incomplete data on length at recapture; therefore, freshwater zone lengths were interpreted as an indication of smolt size. The analysis of freshwater zone lengths and other scale measurements were restricted to 2SW salmon owing to the extremely low returns of 1SW salmon to the Connecticut River (Table 1). Cleaned and mounted scales were measured with an Optimas image processing system. Sample sizes are provided in Table 2.

Statistical analysis of freshwater zone lengths was complicated by the lack of a consistent pattern for which stock had the greater zone-length mean. Freshwater zone lengths were compared among years and between stocks with a two-way analysis of variance

(ANOVA). However, the results of this ANOVA are not reported because the interaction term was significant. Instead, a one-way analysis of variance, with stock as the factor, was conducted for each smolt year.

Circuli spacing patterns and post-smolt growth

The spacing of scale circuli deposited during the first year at sea was measured from scales of 2SW salmon returning to the Penobscot and Connecticut rivers. The first spacing was measured between the first circulus of the post-smolt growth zone and the next circulus, and all successive pairs were measured until the end of the post-smolt growth zone. The end of the zone was recognized when circuli spacings began to widen a second time, indicating the beginning of the second sea summer (Fig. 2). All measurements were made along the 360° axis of the scale.

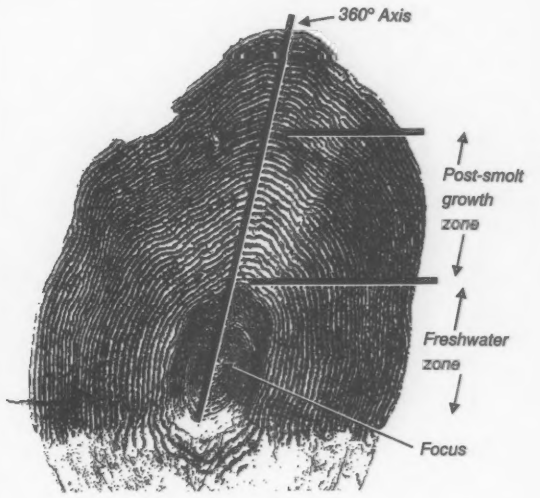

Figure 2
A scale from an Atlantic salmon, *Salmo salar*, with measurement axis and growth zones marked.

Growth during the post-smolt period was evaluated from the circuli spacings in three regions of the scale. We used the spacing patterns as growth indices because, in salmonids and other fish, scale intercirculi spacing is directly related to growth (Doyle et al., 1987; Barber and Walker, 1988; Fisher and Pearcy, 1990). Three regions of the scale were selected to correspond with seasons of the calendar year. The circuli pair spacings used to represent the "spring" period, or first entry of salmon into the marine environment, was fixed to pairs "two" through "six" (Fig. 3). The "summer" period, or the period of maximum growth, was represented by the five widest and contiguous mean spacings. The first sea "winter" period was represented by the five narrowest and contiguous mean spacings. The general assumption that regions of the scale are associated with seasons of the year is supported by the analysis of post-smolt scales from tagged fish and ocean recaptures (Friedland et al., 1993). The three growth zones were identified from the patterns of mean spacings of circuli pairs from all the data for a smolt year cohort and sea-age. This approach was used because it was not possible to identify seasonal growth zones in the spacing patterns for all individuals because of the variability of these patterns.

Cumulative growth during the post-smolt period was represented by the number of circuli in the post-smolt growth zone and the length of the zone itself. A circuli count was determined for each cohort and sea-age group. The count was based on the mean circuli spacing patterns also used to identify growth zones. The count consisted of the number of circuli from the end of the freshwater zone to the first circulus of the third winter circuli pair. The post-smolt

Table 2
Sample sizes and post-smolt growth-zone circuli counts for 2SW Atlantic salmon returns to the Penobscot (Pen) and Connecticut (Conn) Rivers.

Smolt year	Sample size		Circuli count	
	Pen	Conn	Pen	Conn
1977	75	25	26	22
1978	65	77	20	24
1979	75	168	24	21
1980	65	24	24	24
1981	75	9	26	17
1982	75	52	26	20
1983	75	81	27	20
1984	40	45	25	21
1985	108	186	28	22
1986	74	70	27	22
1987	51	75	23	24
1988	64	170	26	23
1989	83	121	26	23
1990	95	179	26	22
Mean			25	22

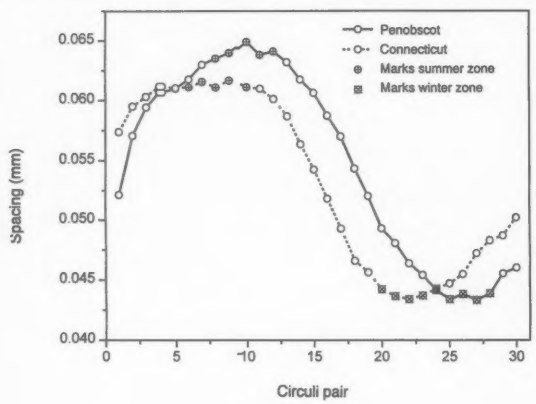

Figure 3

Grand means of circuli spacing versus circuli pair for 2SW returns to the Penobscot and Connecticut rivers. Circuli pairs of summer and winter growth zones are marked as examples.

growth zone length was taken as the distance from the last circulus in the freshwater zone to the outer circulus of the third circuli pair of the winter zone measured along the 360° axis of the scale (Fig. 2). This distance reflects the average spacing of circuli and the number of circuli deposited during the post-smolt period.

Comparison of post-smolt growth

Circuli spacing patterns and lengths of the post-smolt growth zone for both the Penobscot and Connecticut stocks were compared by analysis of variance. Circuli spacings for the spring, summer, and winter zones were compared by means of two-way analysis of variance with year and stock as factors. The growth zone of an individual fish was represented by the mean circuli spacing of the growth-zone circuli pairs identified in the pattern of mean spacings for all fish of that smolt year and stock. In all cases, the interaction terms for these ANOVA's were significant and thus the two-way ANOVA results are not reported. Instead, circuli spacings of both stocks were compared with one-way analysis of variance for each smolt year. The length of the post-smolt growth zone for both stocks was also compared for each year with a series of one-way ANOVA's.

The annual variation in circuli spacing growth-zone indices was compared by using Pearson product-moment correlation. The correlation coefficients were computed by using the seasonal growth-index means for the two stocks.

Results

Return rate and cohort age at maturity

Return rates for both 1SW and 2SW salmon were higher in the Penobscot River than in the Connecticut River. The return rate for 1SW salmon averaged 0.97‰ and ranged from 0.36 to 2.20‰ for the Penobscot stock, whereas for the Connecticut stock the return rate averaged 0.03‰ and ranged from 0.0 to 0.12‰ (Table 1). For 2SW salmon, the return rate for the Penobscot stock averaged 4.89‰ and ranged from 1.98 to 12.69‰, whereas in the Connecticut the return rate averaged 1.40‰ and ranged from 0.28 to 5.11‰. Return rates were significantly different between stocks in a paired t-test ($P<0.01$ for both 1SW and 2SW rates). Despite the differences in the level of 2SW return rates between the two stocks, the pattern of annual variation in 2SW return rates of the two stocks was highly correlated ($r=0.88$, $P<0.01$). Peaks in return rate that occurred with the 1978 and 1983 smolt classes are seen in both time series (Fig. 4A). The relation between the two time series is seen clearly in the normalized or Z-transformed data (Fig. 4B). The transform is simply the observation minus the time-series mean divided by the time-series standard deviation.

The 1SW fraction for the Penobscot, which averaged 11% during the study period, was an order of magnitude higher than the fraction observed for the Connecticut River (Table 1). The difference between stocks was highly significant (paired t-test, $P<0.01$).

Smolt size and age

Smolt sizes of 2SW returns, as indicated by the lengths of the freshwater zone, showed no systematic differences between stocks. Mean freshwater zone lengths ranged from 1.000 to 1.243 mm for both stocks (Fig. 5A). Significant differences between freshwater zone lengths were found for 6 of the 14 smolt classes, but of those 6 years, there were equal numbers of years with greater means in the Penobscot and Connecticut stocks (Table 3).

Circuli spacing patterns and post-smolt growth

Considerable variation in circuli spacing was evident between stocks and among years. Annual mean circuli spacing indices had an approximate range of 0.04 to 0.070 mm (Fig. 5, B–D). Spring and summer spacing indices averaged greater than 0.060 mm for both

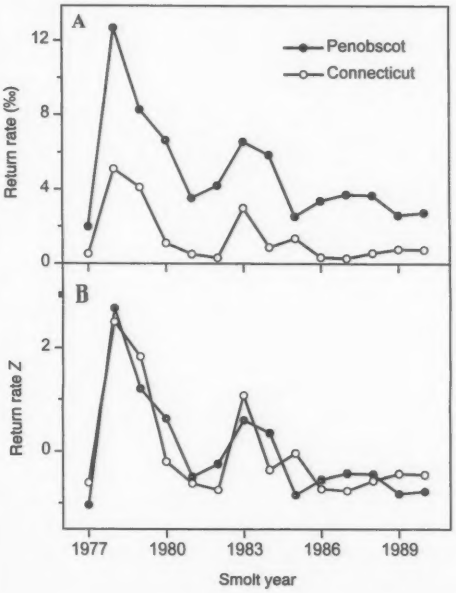

Figure 4

Return rates for 2SW salmon to the Penobscot and Connecticut rivers (**A**). Normalized or Z-transformed return rates for 2SW salmon to the Penobscot and Connecticut rivers (**B**).

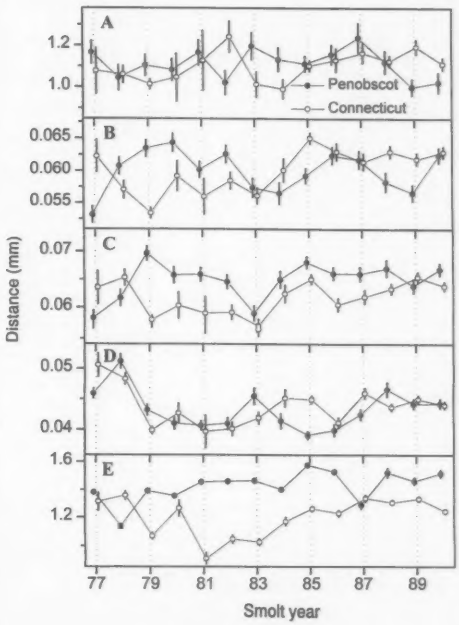

Figure 5

Mean and 95% confidence interval of the following parameters by smolt year: (**A**) freshwater zone length; (**B**) spring growth-zone circuli spacing; (**C**) summer growth-zone circuli spacing; (**D**) winter growth-zone circuli spacing; and (**E**) post-smolt growth-zone length. All measurements are in mm.

the Penobscot and Connecticut stocks, whereas the winter indices averaged less than 0.044 mm. The spring and winter index means were nearly identical for the two stocks, whereas the summer index mean was greater in the Penobscot. The mean number of circuli deposited in the post-smolt growth zone averaged 25 for the Penobscot stock and 22 for the Connecticut stock (Table 2). Post-smolt growth-zone length indices ranged from 0.913 to 1.577 mm and averaged 1.425 mm for the Penobscot stock and 1.204 for the Connecticut stock (Fig. 5E). Differences in the annual seasonal spacing indices and circuli counts were also reflected in the pattern of mean circuli spacings for all years: the Penobscot stock had wider circuli spacing in the summer zone and a greater number of circuli deposited prior to the winter zone (Fig. 3).

Comparison of post-smolt growth

The analyses of variance suggest that post-smolt growth was greater in the Penobscot stock, especially during the summer season. Spring growth indices ranged from 0.053 to 0.065 mm for both Penobscot and Connecticut origin fish (Fig. 5B). Significant differences between Penobscot and Connecticut spring growth-zone means were found for 10 of the 14 smolt classes, and of those 10 years there were equal numbers of years with greater means for the Penobscot and Connecticut stocks (Table 3). Summer growth indices ranged from 0.057 to 0.069 mm for both Penobscot and Connecticut origin fish (Fig. 5C). Significant differences between Penobscot and Connecticut summer-growth-zone means were found for 11 smolt classes, and of those 11 years, 9 were years in which the Penobscot stock had the greater mean (Table 3). Winter growth indices ranged from 0.039 to 0.051 mm for fish of both Penobscot and Connecticut origin (Fig. 5D). Significant differences between Penobscot and Connecticut winter growth-zone means were found for only for 8 of the 14 smolt classes, and of those 8 years, there were equal numbers of years with greater means for Penobscot and Connecticut stocks (Table 3).

Table 3

Probability of one-way ANOVA for stock effect on freshwater zone length (FW zone), seasonal circuli spacing growth indices, and post-smolt growth zone (PS zone). Bolding indicates significance at $P<0.05$. Pen = Penobscot stock; Conn = Connecticut stock.

Smolt year	FW zone	Circuli spacing			PS zone
		Spring	Summer	Winter	
1977	0.131	**0.000**	**0.005**	**0.000**	**0.003**
1978	0.659	**0.009**	**0.011**	**0.049**	**0.000**
1979	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
1980	0.529	**0.002**	**0.000**	0.152	**0.000**
1981	0.703	**0.039**	**0.000**	0.487	**0.000**
1982	**0.000**	**0.001**	**0.000**	0.366	**0.000**
1983	**0.000**	0.339	0.066	**0.002**	**0.000**
1984	**0.001**	**0.033**	0.068	**0.004**	**0.000**
1985	0.689	**0.000**	**0.001**	**0.000**	**0.000**
1986	0.473	0.594	**0.000**	0.097	**0.000**
1987	0.081	0.805	**0.002**	**0.000**	**0.010**
1988	0.851	**0.000**	**0.005**	**0.008**	**0.000**
1989	**0.000**	**0.000**	0.149	0.329	**0.000**
1990	**0.001**	0.657	**0.002**	0.758	**0.000**
Years with significant differences					
Pen>Conn	3	5	9	4	12
Conn>Pen	3	5	2	4	2

Table 4

Correlation coefficients (r) between Penobscot and Connecticut river circuli spacing seasonal growth indices. Bolding indicates significance at $P<0.05$, $n=14$.

Seasonal growth index	r	P-level
Spring	–0.263	0.364
Summer	–0.018	0.950
Winter	**0.535**	**0.049**

Cumulative growth during the post-smolt year appeared greater in the Penobscot stock. The post-smolt growth zone circuli counts were significantly higher in the Penobscot stock ($P<0.01$). Post-smolt growth zone lengths ranged from 0.913 to 1.577 mm for both Penobscot and Connecticut origin fish (Fig. 5E). Significant differences between Penobscot and Connecticut spring growth-zone means were found for all 14 smolt years, and of these, 12 were years in which the Penobscot stock had a greater mean than the Connecticut stock (Table 3).

Annual variation in circuli spacing was similar for two stocks for one of the three post-smolt growth zones. The correlation coefficient for winter spacing indices was significant, whereas the correlation coefficient for spring and summer indices was not significant (Table 4).

Discussion

The Penobscot and Connecticut stocks exhibited similar interannual patterns of 2SW survivorship despite significant differences between the two stocks in magnitude of survival rate and maturation fraction. Therefore, the sets of conditions affecting the two stocks during the post-smolt year must to some degree intersect to account for the similarity in the survival-rate time series. At the same time, however, there must also be significant differences in these condition sets to account for the significantly lower survival and maturation fraction found for the Connecticut stock. We have found it instructive to consider those factors that appear to be similar and those that appear to be different for the two stocks.

The scales from Penobscot and Connecticut fish returns had similar freshwater zone lengths, circuli spacing indices in the spring and winter, and a correlated pattern of annual variability between winter growth indices. These similarities should be interpreted in respect to the correlation in annual 2SW survivorship. The survivorship of North American multiseawinter stocks has been related to ocean conditions in the Labrador Sea during winter (Friedland et al., 1993). It has been hypothesized that stocks emanating from various rivers in North America intermix and are acted upon by a common set of survival conditions during the winter season. The coherence of the survival time series for the Penobscot and Connecticut stocks, as well as for other North American stocks, is considered evidence that stocks converge on the same overwintering ground. Scale analysis shows that annual variation in growth indices during winter were correlated, which would be consistent with the assertion that these fish were in the same location during that season. The lack of correlation between spring and summer indices suggests that the fish from the respective stocks were acted upon by differing conditions, possibly while they resided in different areas. These data suggest that fish from the Penobscot River are not fully mixed with fish from the Connecticut River until the winter season, thus supporting the survival hypothesis for all North American stocks in general.

Though smolt sizes, as inferred by the freshwater zone lengths of the scales, were similar for the two stocks, we can not conclusively eliminate freshwater effects from contributing to observed differences in survival. There is a large body of evidence that

illustrates the influence of smolt-size and condition and stocking circumstances on the return rates and yields of salmon stocks (Ward et al., 1989; Hvidsten and Johnsen, 1993; Farmer, 1994; Lundqvist et al., 1994). We lack smolt size information on the fish that did not survive; they may have had a different freshwater zone length-size frequency than that observed for the survivors. Smolt age composition was similar each year and appears unrelated to the differences between stocks. However, the trend in smolt age composition is not similar to the time-series trends in survival and maturity for the two stocks and should be considered along with other factors when evaluating long-term changes in stock performance (Friedland et al., 1993).

Summer circuli spacing and post-smolt growth-zone length data suggest that the Penobscot fish grew faster than the Connecticut fish as post-smolts. These differences may have influenced survivorship and maturation. These data suggest that fish from the Connecticut stock grew more slowly during the post-smolt year than did Penobscot fish, matured as 1SW less frequently, and were more vulnerable to mortality. It is generally accepted that larger individuals are less vulnerable to predation (Peterson and Wroblewski, 1984; McGurk, 1986; Anderson, 1988; Miller et al., 1988; Pepin, 1991; L'Abee-Lund et al., 1993). Therefore, smaller, slower-growing Connecticut salmon may be vulnerable to a wider range of potential sources of mortality. For example, under these conditions, we would predict that Connecticut post-smolts would be vulnerable to predators for a longer period of the post-smolt year than would Penobscot post-smolts. Likewise, smaller post-smolts may not effectively compete with other predators for prey or may experience ontogenetic mismatches with prey resources that are also growing or that may be transient in post-smolt habitats (Brodeur, 1991; Healey, 1991; Levings, 1994).

Sea-age at maturation is partly a growth-related phenomenon associated with the seasonal accumulation of lipid stores (Rowe et al., 1991; Thorpe, 1994). In general, maturation at a certain age has been associated with individual growth rate and other causal effects (Alm, 1959; Svedäng, 1991; Thorpe, 1994); however, the effect of sea growth on maturation in salmon has not always been obvious (Power, 1986; Randall et al., 1986; Myers and Hutchings, 1987). Using sea ranching and cage culture experiments with the same genetic stock of salmon, Saunders et al. (1983) reported evidence supporting a hypothesis that first seawinter temperature minima are critical determinants of maturation in salmon. This work was further supported by Herbinger and Newkirk (1987) who described a relationship between 1SW maturation and favorable (or perhaps minimum) winter growth. However, the specificity of seasonal growth effects can be challenged by other experimental evidence that shows that spring growth can influence 1SW maturation (Thorpe et al., 1990). In an analysis of the Penobscot stock, Friedland and Haas (1996) showed that maturation fraction varies with summer growth rate of the cohort as indicated by circuli spacing indices for 2SW returns. This finding is further supported by our comparison of Penobscot and Connecticut fish which shows that the stock with the greater summer growth had produced a higher percentage of mature 1SW fish.

How an environmentally driven maturation mechanism would optimize age at maturation is not clear. For salmon stocks with complex maturation age structures, early maturing fish (1SW) are predominantly males; egg-producing females more frequently mature at a later age when their egg production is maximized. Therefore, a shift in age at maturity allows a brood class to receive genes from more than one spawning cohort without significant loss of egg production. This plasticity in spawning age ensures that genes move within the population while remaining robust to environmental effects on the deposition of female gametes, which are limiting (Stearns and Crandall, 1984; Stearns, 1992). However, Atlantic salmon exhibit a wide range of maturation age structures (Power, 1981; Saunders, 1981; Saunders and Schom, 1985) suggesting within-population heterozygosity may also be maintained by protracted freshwater residency that allows many brood years to contribute to a smolt run in a given year.

Genetic influences have also been shown to affect stock-specific patterns of age at maturity (Saunders et al., 1983; Thorpe et al., 1983). However, genetic factors are unlikely to explain the differences between the Penobscot and Connecticut stocks because the Connecticut stock is derived predominantly from the Penobscot gene pool (Rideout and Stolte, 1988). When the Connecticut River broodstock was developed, gametes from Canadian and U.S. origin (Penobscot River broodstock) donor stocks were used. However, the crosses with Canadian genetic sources, as demonstrated with tagging, produced virtually no progeny; therefore it can be concluded that the Connecticut broodstock is principally derived from the Penobscot River broodstock.

The systematic differences in growth, survival, and maturation between these two stocks may be related to their post-smolt migrations. When salmon first enter the marine environment, they move by active and passive mechanisms (Jonsson et al., 1993). Because of the differences in the timing of the smolt migration, the starting point of the post-smolt feed-

ing migration, and changes in the ecology of the ocean habitat of salmon, Penobscot and Connecticut smolts are probably exposed to different predator and prey communities during the course of their migrations. These differences would be expected to manifest themselves in growth differences, and as a consequence, in differences in survival and maturation of the two stocks.

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Abstract.—The Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, is a small coastal shark that is harvested in both directed and nondirected fisheries throughout its range. Because pups of this species are found both along the southeastern U.S. Atlantic coast and the Gulf of Mexico, it is possible that multiple isolated breeding stocks exist. Restriction fragment length polymorphism analysis of mitochondrial DNA was used to test the hypothesis that Atlantic sharpnose sharks from the U.S. Atlantic coast and the western Gulf of Mexico have identical mitochondrial haplotype frequencies and therefore no apparent genetic stock structure. Seven mitochondrial haplotypes were detected among 52 individuals. The distribution of haplotypes between samples did not differ significantly from homogeneity (P= 0.694), indicating that the null hypothesis of a single breeding population could not be rejected.

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Mitochondrial DNA diversity and divergence among sharpnose sharks, *Rhizoprionodon terraenovae*, from the Gulf of Mexico and Mid-Atlantic Bight*

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The Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, is a small (maximum length 110 cm total length) coastal shark that inhabits the east coast of North America from New Brunswick, Canada, to Yucatan, Mexico (Compagno, 1984). This species is abundant along the southern U.S. Atlantic coast and is second only to the sandbar shark, *Carcharhinus plumbeus*, in longline catches in Virginia (Musick et al., 1993). It supports a large recreational fishery off Texas (Parrack[1]) and is an important species in the Mexican shark longline fishery (Applegate et al., 1993). In addition to being caught in directed fisheries, the Atlantic sharpnose shark is frequently taken by shark longliners targeting large coastal species (Branstetter and McEachran, 1986; Russell, 1993) as well as by commercial shrimp trawlers (Branstetter, 1981; Parrack[1]); however, the implementation of turtle excluder devices (TED's) has produced the additional benefit of reducing bycatch of sharks (Branstetter[2]). Atlantic sharpnose sharks travel in sex-segregated schools, as noted by the disparate sex ratios of adults captured by longlines (Branstetter, 1981; Musick et al., 1993). The gestation period for this species is about ten to twelve months, and parturition takes place from April to June in the northern Gulf of Mexico (Branstetter, 1981; Parsons, 1983) and from May to June in South Carolina (Castro, 1993).

The most recent fishery management plan for sharks in the coastal Atlantic waters of the United States (NMFS[3]) divides sharks into three categories for management purposes: pelagic species, large coastal species, and small coastal species. Currently catches of small coastal species (predominantly the Atlantic sharpnose shark) are not regulated

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because catch rates are assumed to be at or below maximum sustainable yield and because life history parameters predict a relatively high recruitment rate for this species in comparison to the large coastal species targeted by the U.S. Atlantic shark longline fishery (NMFS[3]). Recently Cortés (1995) challenged this assessment on the basis of a reevaluation of life history characteristics relevant to recruitment (age at maturity, fecundity, and longevity) and suggested that the Atlantic sharpnose shark may be more vulnerable to overfishing than was previously assumed.

Proper management of this species requires not only accurate estimates of standing stock and recruitment values but also an understanding of the reproductive population structure of the species. The observation that pups of this species are found both in the South Atlantic Bight as well as in the Gulf of Mexico, coupled with the small size and apparent lack of significant longshore migration, suggests that there may be isolated breeding populations of this species. Information on stock structure of marine fishes has traditionally relied on two approaches: tag and recapture studies and analyses of genetic variation. Although considerable information has been obtained on the movements of large sharks by means of tagging (Casey and Kohler, 1990), these tagging studies have generally neglected smaller species of sharks. Furthermore, to our knowledge the genetic structure of any population of small coastal shark has not been investigated. This study tests the hypothesis of genetic homogeneity in allele frequency in Atlantic sharpnose sharks between the Gulf of Mexico and Mid-Atlantic Bight by using restriction fragment haplotypes of mitochondrial DNA (mtDNA).

Materials and methods

Atlantic sharpnose sharks were collected with research longlines in the Mid-Atlantic Bight (n=23) as part of an ongoing shark research program of the Virginia Institute of Marine Science, from the recreational fishery of southern Texas (n=21) and from artisanal longline vessels from Veracruz, Mexico (n=8) (Fig. 1). Heart tissue samples from Atlantic sharpnose sharks caught in the Mid-Atlantic Bight were placed into cryovials and stored under liquid nitrogen in the field. In Texas and Mexico, whole hearts were collected on wet ice and stored frozen at (–20°C) until shipped to Virginia. All samples were stored at –70°C.

Mitochondrial DNA was isolated from tissue by following the rapid isolation protocol of Chapman and Powers (1983). Aliquots of mtDNA were digested with ten restriction enzymes (*Ava* I, *Ava* II, *Ban* I, *Bcl* I, *Bst*E II, *Dra* I, *Hin*d III, *Hpa* I, *Sca* I, and *Xho* I) by following the manufacturers' instructions. Restriction fragments were separated on 1.0% horizontal agarose gels run at 2V/cm overnight, then transferred after electrophoresis to a nylon membrane by means of Southern transfer according to the protocols of Sambrook et al. (1989). Filters were hybridized with highly purified mtDNA from tiger shark, *Galeocerdo cuvier,* nick-translated with biotin-14-dATP, and visualized with the BRL BlueGene Nonradioactive Nucleic Acid Detection System.

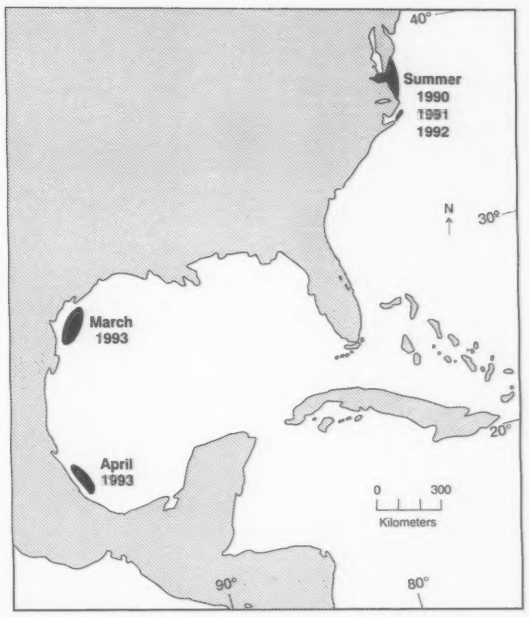

Figure 1

Locations and dates for collection of sharpnose shark, *Rhizoprionodon terraenovae.*

Fragment patterns were scored for each restriction enzyme and each individual was assigned a composite genotype based on the fragment patterns for all enzymes (Tables 1 and 2). The nucleon (haplotype) diversity was calculated for each sample and for the composite of all samples following Nei (1987). Nucleotide sequence diversity was calculated following the site approach of Nei and Miller (1990). Chi-square significance of the difference in genotypic frequencies between samples was computed by using the randomization protocol of Roff and Bentzen (1989). Nucleotide sequence diversities and divergences were calculated by using the REAP statistical analysis package (McElroy et al., 1991).

Table 1

Estimated size in kilobase pairs of mitochondrial DNA restriction fragments for various restriction enzymes in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*.

Ava I		*Ava* II	*Ban* I	*Bcl* I		*Bst*E II	*Dra* I		*Hin*d III	*Hpa* I				*Sca* I	*Xho* I
(A)	(B)	(A)	(A)	(A)	(B)	(A)	(A)	(B)	(A)	(A)	(B)	(C)	(D)	(A)	(A)
7.53	7.53	11.12	11.54	6.62	6.62	6.23	3.14	2.68	6.06	4.84	4.84	5.57	4.84	9.85	11.30
5.17	7.09	2.43	5.44	4.10	4.10	6.09	2.68	2.50	3.83	4.03	3.55	4.03	4.76	5.89	5.32
1.92	1.02	1.60	—	2.26	3.08	1.57	2.08	2.08	2.43	3.43	3.43	3.43	3.43	1.08	—
1.02	8.34	0.64	16.98	1.87	2.26	1.54	2.08	2.08	2.43	2.09	2.09	2.09	2.09	—	16.62
0.83	—	0.55		1.21	0.79	0.84	1.75	1.75	0.80	1.18	1.18	1.18	1.18	16.82	
—	16.48	—		0.79	—	0.65	1.56	1.56	0.68	0.73	0.73	—	—		
16.47		16.33		—	16.85	—	1.14	1.14	—	—	0.45	16.30	16.30		
				16.85		16.92	1.14	0.98	16.23	16.30	—				
							0.98	0.98			16.27				
							—	0.57							
							16.55	—							
								16.32							

Results

Ten restriction enzymes produced an average of 50 restriction fragments with a survey of 288 base pairs (bp) or 1.74% of the 16.6 kb mtDNA molecule (Table 1). Seven haplotypes were detected, resulting in a nucleon diversity of 0.640 and an overall nucleotide sequence diversity (NSD) of 0.13% (Table 2; Fig. 2). Four of the ten restriction enzymes revealed multiple restriction patterns; one enzyme, *Hpa* I, detected four different patterns. The single most common haplotype was found with similar frequencies in each sample and in each year within the Atlantic sample (range=0.50–0.67), and three less common haplotypes also occurred in all three geographic samples. Three rare haplotypes, each found in a different individual, were equally divided among the three sampling locations. Each haplotype differed from the common pattern by the gain or loss of a single restriction site (Fig. 2.) The chi-square probability of haplotype homogeneity among samples (Roff and Bentzen, 1989) was 0.694, indicating that the samples could have been drawn from a single population of mtDNA haplotypes. The nucleotide sequence divergences between the three samples, corrected for within sample diversity, were all less than 0.01%.

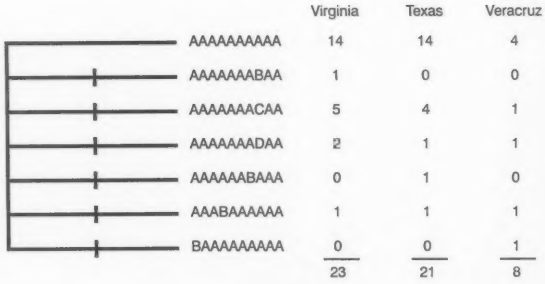

Figure 2

Composite mtDNA haplotypes, inferred phylogenetic relationships among haplotypes (vertical hatches represent restriction site differences), and distribution of haplotypes in samples of Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Composite haplotypes consist of restriction fragment patterns for the following enzymes (left to right): *Ava* I, *Ava* II, *Ban* I, *Bcl* I, *BstE* II, *Dra* I, *Hin*d III, *Hpa* I, *Sca* I, and *Xho* I.

Table 2

Nucleon diversity and percent nucleotide sequence diversity in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*.

Sample source	Nucleon diversity	Nucleotide sequence diversity (%)
Virginia	0.597	0.120
Texas	0.538	0.105
Veracruz	0.788	0.175
Total	0.640	0.133

Discussion

The results of this study indicate that historically there has been sufficient gene flow among sharpnose

sharks from the Gulf of Mexico to the Mid-Atlantic Bight to prevent significant divergence in mitochondrial DNA haplotypes. The frequencies of the most common alleles, as well as the occurrences of rare alleles, were nearly identical in each of the three samples. The nucleon and nucleotide sequence diversities were also similar among samples. The hypothesis that Atlantic sharpnose sharks collected from locations as distant as Veracruz and Virginia were members of a single homogeneous gene pool could not be rejected.

The distribution of mtDNA haplotypes has been used previously to infer patterns of gene flow in several other commercially important shark species in the Gulf of Mexico and southeastern (U.S.) Atlantic coast (reviewed in Avise, 1992). Gene flow in fishes is accommodated both by the active movement of juveniles and adults, as well as by the passive movement of eggs and larvae. Significant differences in mtDNA haplotype frequencies have been detected in species with limited adult migration and demersal eggs (marine toadfishes, *Opsanus* spp.; Avise et al., 1987) as well as in those with pelagic eggs and larvae (black sea bass, *Centropristis striata;* Bowen and Avise, 1990; and menhaden, *Brevoortia* spp., Bowen and Avise, 1990).

Sharpnose sharks are nektonic from the moment of parturition; therefore, gene flow is accommodated only by the active movements of juveniles and adults. Significant differences in haplotype frequencies were detected in redfish (*Scianops ocellatus*; Gold et al., 1993) of the Gulf of Mexico and southeast U.S. Atlantic coast but not in the hardhead catfish (*Arius felis;* Avise et al., 1987), two species with large active adults but with presumably little passive transport of eggs and larvae. In addition, Heist et al. (1995) detected no heterogeneity in mtDNA haplotype frequencies in the sandbar shark, *Carcharhinus plumbeus*, over the same geographic range.

In menhaden, the presence of two groups of genetically divergent mtDNA haplotypes in the Atlantic was interpreted as indicating complete isolation of these two groups in the past, followed by a mixture of stocks with divergent mtDNA haplotypes (Bowen and Avise, 1990). The close relationships among all haplotypes detected in the Atlantic sharpnose shark is consistent with the hypothesis of a single evolutionary lineage with no historical subdivision.

The lack of genetic divergence among Atlantic and Gulf of Mexico sharpnose sharks can not prove that separate stocks do not exist. An exchange rate of a small number (<20) of females per generation between isolated breeding populations is enough to prevent drift from establishing significant heterogeneity in allele frequencies (Allendorf and Phelps, 1981). Therefore fishery-relevant stocks can be maintained in the absence of statistically significant genetic divergence. Furthermore, if a single population has recently diverged into multiple stocks, there may not have been sufficient time for a significant level of genetic divergence to have become established. Perhaps by examining genetic characters that evolve more rapidly than whole mitochondrial DNA (such as direct sequencing of the mitochondrial control region or microsatellite analysis) stock structure may be eventually detected in this species. The only way, however, to determine the current level of gene flow in this species may be through a tag and recapture program. This information is necessary to determine whether regional exploitation of this species will be compensated by immigration from other regions and whether regional (state) regulations will be an effective means of conservation.

In order to perform robust tests of hypotheses concerning gene flow in organisms, the markers used must have sufficient intraspecific variation so that differences in the frequencies of alleles can be assessed between regions. The level of intraspecific variation in the Atlantic sharpnose shark (NSD= 0.13%) is considerably higher than the NSD of 0.036% reported by Heist et al. (1995) in the sandbar shark, *Carcharhinus plumbeus*, although lower than that detected by Heist et al. (1996) in the shortfin mako, *Isurus oxyrinchus* (NSD=0.38%). Although the number of individuals surveyed in this study is small, the similar amount of variation detected within each sample and the close agreement in frequencies between regions strongly suggest mtDNA haplotype homogeneity between sharpnose sharks of the Mid-Atlantic Bight and Gulf of Mexico. This study has demonstrated that this small coastal shark, with no passive larval transport, nevertheless exhibits mtDNA haplotype homogeneity across a broad geographic range.

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Gillnetting in southern New Zealand: duration effects of sets and entanglement modes of fish

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Abstract.—This study examined the catch from gill nets set on nearshore rocky reefs around the Kaikoura Peninsula on the east coast of the South Island of New Zealand. The combined catch of 114 net sets of three net mesh sizes (2.5", 3.5", and 4.5") was analyzed for the mode of entanglement of captured fish and for duration effects on fish. Fusiform species were commonly gilled and wedged, whereas laterally compressed species usually became tangled by fins or spines; these patterns appeared to be a consequence of the behavioral and morphological characteristics unique to each species. The average fork length of caught fish increased with mesh size for gilled and wedged fish but not for those that were tangled. Within each mesh size, entangled fish tended to have the largest mean fork length, gilled fish were intermediate in mean fork length, and wedged fish had the smallest mean fork length. Nets of 2.5" mesh size caught the most fish over all set durations. There was no significant difference between a 6-hour set and a 15-hour set in the number of fish or number of species caught. The proportion of damaged fish in the landed catch was small for nets of all three mesh sizes set for six hours but increased markedly for set times that were longer. Clearly both mesh size, as well as morphological and behavioral differences between species affect the susceptibility of individual fish to gill nets.

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Different species of fish are not equally vulnerable to a given method of fishing. Gill nets, in particular, are highly selective in terms of the sizes and species of fish they catch (Hamley, 1975; Boy and Crivelli, 1988). There are many factors, however, other than the species or size of a fish that can influence the susceptibility of a fish to being caught in a gill net. Hamley (1975) listed these factors as the reaction of fish to nets, the different behavior of fish around nets, the type of net construction, the hanging coefficient, net saturation and characteristics of nets, such as their visibility, elasticity of meshes, and filament size. Dimensional characteristics of fishes, such as length-weight relationships (Kipling, 1957), length-condition relationships (Regier, 1969), and length-girth relationships (Kawamura, 1972), can also influence selectivity.

It is generally agreed that a given mesh size provides a size selection for a particular species that is characterized by a lower size limit, below which fish are small enough to pass through the mesh without hindrance, and by an upper size limit, above which fish are too large to enter the mesh and become entangled (Hamley, 1975). Between these limits the length-frequency distribution of the catch is approximately normal, with a mode at the length where the corresponding girth measure is slightly greater than the mesh perimeter (McCombie and Fry, 1960; Berst, 1961; Garrod, 1961; McCombie and Berst, 1969).

The number of fish caught in gill nets does not necessarily increase in direct proportion to the time that nets are in the water (Kennedy, 1951). Van Oosten (1935) showed that gill nets left for eight nights caught only 47 percent more fish than the same nets left for four nights, whereas if the catch increased in direct proportion to the time fished, the increase would have been 100 percent. The presence of captured, struggling fish and of dead fish may result in the efficiency of gill nets decreasing with time (Kennedy, 1951).

The analysis of catches of fish taken in gill nets is complicated by the passive nature of this type of fishing gear (Berst and McCombie, 1963). Several factors affect gill-net catches, such as the movement of fish, the shape and structure of the fish, and the associative pattern or grouping of the individuals of any species or assemblage of species (Moyle, 1950).

The aim of the present study was to analyse the size range and abundance of the most common fish species in gill-net catches from nearshore reefs in southern New Zealand. The data for this analysis were derived from the catch of nets used for comparison of reef fish populations previously assessed by visual

survey (Hickford and Schiel, 1995) and from gill nets that were used for behavioral observations. By recording the morphological features of the catch, along with the form of entanglement, the primary factors that determine the vulnerability of individual species to particular mesh sizes could be identified. Analysis of the quantity and quality of the catch landed from gill nets set for various periods should yield an optimum set time that will maximize landings and reduce wastage.

Materials and methods

The gillnet catch analyzed in this study was pooled from several experiments. Consequently, the resulting sampling design is not orthogonal. The netting was done on rocky reefs around the Kaikoura Peninsula on the east coast of New Zealand's South Island (42°25'S, 173°42'E) from 8 January 1993 to 26 February 1993. The nets (Table 1) were set from a 6-meter runabout and hauled in by hand. Each net was set in a random direction and the ends were anchored with weights and marked with surface buoys. At least 10 meters separated any two nets. The nets were set on the bottom at depths ranging from 3 to 15 meters and for periods of 11–17 hours. At all sites the benthic habitat type had been described (Hickford and Schiel, 1995) and the fish populations had been surveyed with visual transects by divers immediately before the nets were set. At the end of all sets, the nets were placed in bins and brought back to the laboratory with fish still entangled in the mesh for analysis of the catch. The combined catch of 114 net sets of three mesh sizes over a single known habitat type (rocky pinnacles, mixed algae [Hickford and Schiel, 1995]) was analyzed.

As each fish was removed from the net, its species and fork length (mm) were recorded as was the method by which each fish had become trapped in the mesh. If a fish was held by the mesh encircling its body between the posterior edge of its operculum and the base of its pectoral fin, it was determined to have been "gilled." If the mesh encircling the body was posterior to the base of the pectoral fin, the fish was determined to have been "wedged." If a fish was held because mesh had snagged an appendage, such as the fins, spines, teeth, or maxilla, or if the fish's struggling had simply enveloped it in the mesh, it was described as "tangled." Careful handling of the nets resulted in very few "drop-outs" from the net. However, any fish that were loose in the net were excluded from subsequent entanglement analysis.

Entanglement data were collated for each species in each mesh size. Because the species composition of individual net sets was so variable and because many species were caught only in a small proportion of sets, the analyses of entanglement data were restricted to the five most commonly caught species. This produced a 5×3×3 contingency table, in which the number of fish caught were categorized according to species, mesh size, and entanglement mode. This table was analyzed by using a log-linear model that required thirteen iterations for the G-value to be minimized ($|\Delta G| < 0.001$; Sokal and Rohlf, 1981). The odacid *Odax pullus* was the only species caught in large enough numbers across most net sets for individual statistical analysis of entanglement to be done.

The duration of each net set was recorded. Two set times were chosen for analysis: a 6-h daytime set from late morning to late afternoon and a 15-h night set from late afternoon to early morning. The number of fish and number of species caught during each set were compared. A comparison of the capture rates of common species was also made between day and night sets and between mesh sizes. Each fish caught was given a condition index according to the degree of damage it had sustained while in the net (Table 2).

Results

The 114 net sets caught 1,165 fish from 14 families (Table 3). The odacid *Odax pullus* (46% of the total

Table 1

The dimensions of the gill nets used in fishing during this study. Mesh size is given in inches by the manufacturers and is measured as the diagonal length of a stretched mesh. Filament size is the diameter of the monofilament.

Net and mesh dimension	Measurement		
Net length (m)	30	30	30
Net height (m)	1.80	1.75	1.72
Mesh size (inches)	2.5	3.5	4.5
Filament size (mm)	0.36	0.48	0.58

Table 2

Descriptions of the indices used to categorize the condition of fish landed in gill nets.

Condition index	Damage
No damage	Chafing or scale loss from contact with gill net
Minor damage	Minor lesions; fin or eye damage
Major damage	Major lesions; flesh loss or sea lice damage
Severe damage	Loss of skeletal material

Table 3

The species, common name, fisheries code, and number of fish caught in each of the three mesh sizes and in total. The number of individual net sets are shown in parentheses under the mesh size.

Family and species	Common name	Fisheries code	No. of fish: Mesh size 2.5" (29)	3.5" (30)	4.5" (55)	Total no. (114)
Myliobatidae						
Myliobatis tenuicaudatus (Hector, 1987)	Eagle ray	EGR	0	1	0	1
Moridae						
Lotella rhacinus (Bloch and Schneider, 1801)	Rock cod	ROC	2	1	0	3
Pseudophycis bachus (Bloch and Schneider, 1801)	Red cod	RCO	2	4	1	7
Carangidae						
Pseudocaranx dentex (Bloch and Schneider, 1801)	Trevally	TRE	0	0	1	1
Trachurus declivis (Jenyns, 1841)	Jack mackerel	JMA	1	1	2	4
Arripidae						
Arripis trutta (Bloch and Schneider, 1801)	Kahawai	KAH	88	6	13	107
Aplodactylidae						
Aplodactylus arctidens Richardson, 1839	Marblefish	GTR	56	45	19	120
Cheilodactylidae						
Cheilodactylus spectabilis (Hutton, 1872)	Red moki	RMO	0	0	5	5
Nemadactylus macropterus (Bloch and Schneider, 1801)	Tarakihi	TAR	0	1	0	1
Latrididae						
Latridopsis ciliaris (Bloch and Schneider, 1801)	Blue moki	MOK	115	40	29	184
Latridopsis forsteri (Castelnau, 1872)	Copper moki	CMO	0	4	2	6
Latris lineata (Bloch and Schneider, 1801)	Trumpeter	TRU	2	0	0	2
Mendosoma lineatum Guichenot, 1849	Telescope fish	TEL	1	0	0	1
Mugilidae						
Aldrichetta forsteri (Cuvier and Valenciennes, 1846)	Yellow-eyed mullet	YEM	22	1	0	23
Labridae						
Notolabrus celidotus (Bloch and Schneider, 1801)	Spotty	STY	7	0	0	7
Notolabrus fucicola (Richardson, 1840)	Banded wrasse	BPF	46	7	5	58
Pseudolabrus miles (Bloch and Schneider, 1801)	Scarlet wrasse	SPF	2	2	0	4
Odacidae						
Odax pullus (Bloch and Schneider, 1801)	Butterfish	BUT	462	72	7	541
Pinguipedidae						
Parapercis colias (Bloch and Schneider, 1801)	Blue cod	BCO	6	3	1	10
Gempylidae						
Thyrsites atun (Euphrasen, 1791)	Barracouta	BAR	0	1	0	1
Istiophoridae						
Seriolella brama (Günther, 1860)	Blue warehou	WAR	45	31	1	77
Monacanthidae						
Parika scaber (Bloch and Schneider, 1801)	Leatherjacket	LEA	0	0	2	2
		Total	857	220	88	1,165

catch), the latrid *Latridopsis ciliaris* (16%), and the aplodactylid *Aplodactylus arctidens* (10%) represented most of the total catch. For the five most commonly caught species, the degree of association between mesh size and method of capture differed for different species (G=81.395, $\chi^2_{0.05[16]}$=26.296, P<0.001). For example, the coastal labrid *Notolabrus fucicola* was mostly gilled in the 2.5" mesh; few of these fish were caught in the larger mesh sizes, and few were caught by wedging and tangling (Table 4). In contrast, the large, slow-moving latrid *L. ciliaris* was mostly tangled in the 2.5" mesh, gilled and tangled in approximately equal numbers in the 3.5" mesh, and mostly gilled in the 4.5" mesh. *Odax pullus* was mostly gilled in the 2.5" and 3.5" meshes and few were caught in the 4.5" mesh. The bottom-dwell-

Table 4

Observed catch frequencies by mode of entanglement for five commonly caught species.

Species	Mesh (inches)	Observed catch			
		Gilled	Wedged	Tangled	Total
Notolabrus fucicola	2.5	39	4	1	44
	3.5	4	1	1	6
	4.5	2	1	1	4
	Total	45	6	3	54
Odax pullus	2.5	317	74	41	432
	3.5	35	25	3	63
	4.5	2	1	1	4
	Total	354	100	45	499
Aplodactylus arctidens	2.5	18	5	28	51
	3.5	24	14	4	42
	4.5	5	10	2	17
	Total	47	29	34	110
Arripis trutta	2.5	61	13	9	83
	3.5	1	1	3	5
	4.5	4	1	3	8
	Total	66	15	15	96
Latridopsis ciliaris	2.5	18	11	60	89
	3.5	15	1	19	35
	4.5	16	5	3	24
	Total	49	17	82	148

ing *A. arctidens* was mostly tangled in the 2.5" mesh, but most fish were gilled and wedged in the 3.5" and 4.5" mesh sizes. The pelagic *Arripis trutta* was mostly gilled in the 2.5" nets, but the number of fish gilled and tangled was approximately equal in the 3.5" and 4.5" nets.

Overall, the mean fork length of each species increased with mesh size for gilled, wedged, and tangled fish (Fig. 1). For example, the mean fork length of gilled *Arripis trutta* was 240 mm in the 2.5" mesh, 310 mm in the 3.5" mesh, and 505 mm in the 4.5" mesh. There was a similar pattern for this species for tangled fish that averaged 460 mm, 560 mm, and 580 mm for the three mesh sizes respectively. There was considerable variation among species in their size interaction among mesh sizes and form of entanglement. However, for most species within each mesh size, the general pattern was that tangled fish had the largest mean fork length, gilled fish had an intermediate mean fork length, and wedged fish had the smallest mean fork length.

There was a clear transition in the proportion of *Odax pullus* captured by each mode as fork length increased in both the 2.5" and 3.5" mesh sizes (Fig. 2). Too few *O. pullus* were caught in the 4.5" mesh for analysis. Gilled fish were significantly larger than wedged fish ($F_{1,104}$=35.77, P<0.001) in both the 2.5" and 3.5" nets. In the 2.5" mesh, tangled fish were significantly larger than gilled fish ($F_{2,453}$=78.41, P<0.001). Overall, the 3.5" mesh caught significantly larger fish than did the 2.5" mesh ($F_{1,104}$=453.36, P<0.001).

With respect to set duration, the 2.5" mesh caught significantly more fish (all species) than the other mesh sizes over both 6 and 15 hours ($F_{2,12}$=36.96, P<0.001) but there was no significant difference between the two set durations in the number of fish caught (Fig. 3A). The 2.5" mesh size also caught a significantly greater number of species over both set durations ($F_{2,12}$=7.60, P=0.007). Again, there was no significant difference between the two set durations in the number of species caught (Fig. 3B).

There was variation among species in the number of fish caught at different set durations (Fig. 4, A–D). The 2.5" mesh caught significantly more *Odax pullus* per hour over both set durations ($F_{2,12}$=5.40, P<0.05). However, there was no significant difference between the two set times in the number of *O. pullus* caught per hour ($F_{2,12}$=3.57, P=0.08). There was also no significant difference between the three mesh sizes

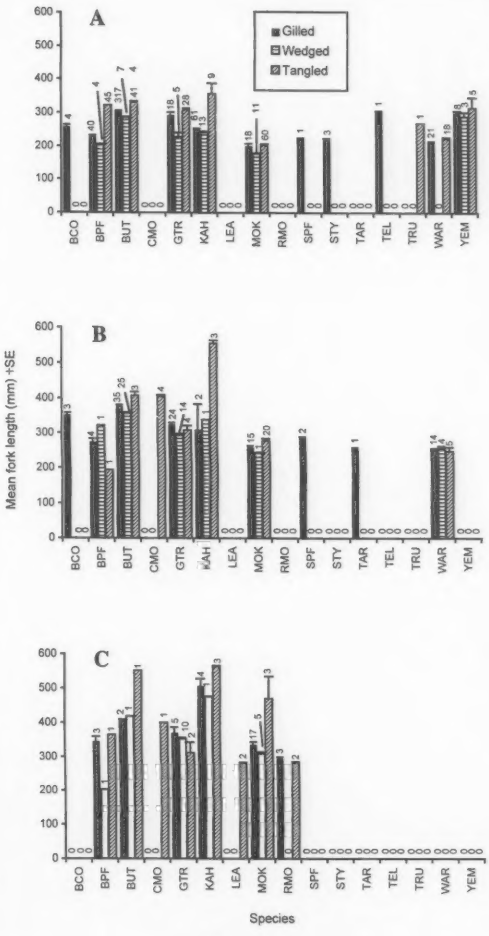

Figure 1

The mean fork length (+1 SE) of fish captured by each entanglement mode in the (**A**) 2.5" mesh, (**B**) 3.5" mesh, and (**C**) 4.5" mesh. n = the number of fish from each species caught in each method. See Table 3 for species codes.

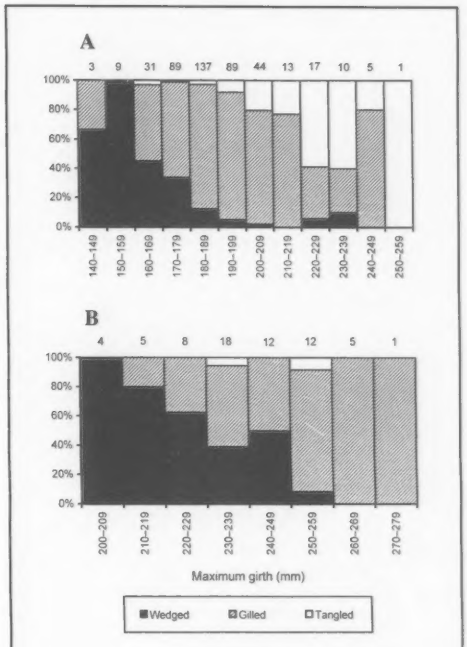

Figure 2

Proportion of butterfish, *Odax pullus*, caught by each entanglement mode in the (**A**) 2.5" mesh and (**B**) 3.5" mesh. n = the number of fish in each size class.

or the two set durations in the number of *Aplodactylus arctidens*, *Latridopsis ciliaris*, or *Arripis trutta* caught per hour (all F values were not significant).

The proportion of damaged fish in the landed catch was small for nets of all three mesh sizes set for six hours but increased markedly for the longer set times (Fig. 5). ANOVA of the condition index of 16 fish selected randomly from each mesh size and each set time showed that fish were significantly more damaged in the longer sets ($F_{1,90}$=19.23, P<0.001), but there was no significant difference among the three mesh sizes in the degree of damage suffered by landed fish ($F_{2,90}$=2.76, P=0.069).

Discussion

Each species showed a distinctive pattern in its form of entanglement in the three mesh sizes. These patterns appear to be a consequence of the behavioral and morphological characteristics unique to each species. For example, *Arripis trutta* were caught mainly by being gilled in the nets. This species is a pelagic carnivore that is dependent on a strong swimming thrust for catching prey. Once gilled, they would be expected to drive forward firmly into the net and to become wedged. The low number of wedged fish for this species may be a result of their firm flesh, which is not easily compressed by the mesh and which may prevent them from entering the net further. Larger fish, despite their greater swimming thrust (Lander, 1969), cannot enter the small mesh sizes far enough to become wedged.

Odax pullus were mostly gilled and wedged in the nets. The low number of *O. pullus* that become tangled was likely the result of the soft fin rays, fused teeth, and small scales typical of this species (Paulin et al., 1989), all of which offer little that will snag on

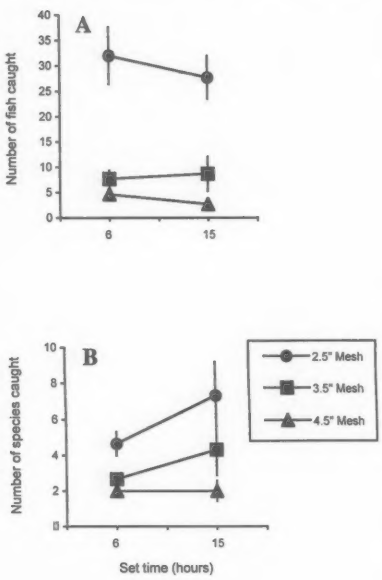

Figure 3

The mean number of fish (**A**) (±1 SE) and the mean number of species (**B**) (±1 SE) landed by the three mesh sizes against time.

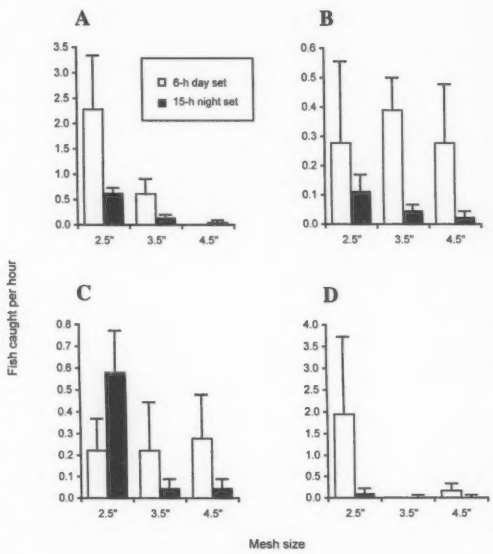

Figure 4

The mean number of fish caught per hour (+1 SE) for four common species in three mesh sizes and in two set durations.

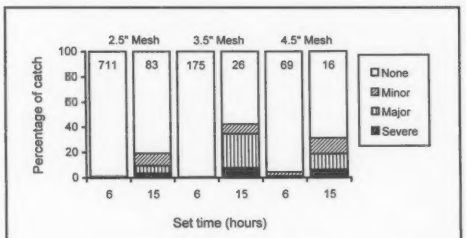

Figure 5

The percentage composition of the catch from nets of three mesh sizes in terms of condition of fish after various set times. n = the number of fish landed by each mesh size after each set duration. See Table 2 for damage categories.

the mesh. However, several other characteristics unique to *O. pullus* make this species very vulnerable to capture by gill nets. The fusiform body shape of this species allows even large individuals to enter the mesh of a gill net to about half their body length before further forward movement is prevented. Their sinuous swimming motion and weak pectorals do not allow them to swim backwards out of a gill net or to stop quickly. This, coupled with the tendency of *O. pullus* to swim below the algal canopy where they are likely to have difficulty detecting the mesh, makes this species one of the most vulnerable to gill nets.

Aplodactylus arctidens were mostly gilled and tangled when caught in the nets. This mode of capture may be due to the strong dorsal spines in this species' anterior dorsal fin which prevent the mesh from passing further along the fish's body. The differences between mesh sizes in the proportions of *A. arctidens* caught by each method may be a result of mesh selectivity. The great number of fish tangled in the 2.5" mesh is probably a result of larger fish becoming tangled by their fins and spines. Small fish caught initially in equivalent numbers in the larger mesh sizes are able to pass through the net unhindered.

Notolabrus fucicola, a labrid species, were mostly gilled when caught in the nets. This is likely to be a result of their labriform swimming motion, which enables them to swim backwards out of the net rather than having to force their way through the mesh. If a labrid's backward motion is not prevented by its gills becoming snagged, it invariably escapes from the mesh. Labrids have also been observed to display a unique rolling motion when first tangled in

the net (Hickford and Schiel, 1995), a motion that often results in a fish freeing itself from the net.

The deep-bodied *Latridopsis ciliaris* were mostly tangled and gilled. The small number of this species that were found wedged in net mesh is probably due to none of the mesh sizes being large enough to allow larger blue moki to enter the nets any further than their gills. The significantly greater number of fish tangled in the 2.5" mesh is a result of larger fish becoming tangled by their large fins and protruding fin rays. Large, laterally compressed fish, such as *L. ciliaris* and *Nemadactylus macropterus*, are not strong swimmers (Doak, 1991). They rely on muscular undulations from head to tail in order to swim, and they brake with their pectoral fins. This weak swimming ability, coupled with their large spiny fins, resulted in *L. ciliaris* often becoming entangled by a single fin rather than being truly enmeshed in the net.

Winters and Wheeler (1990) stated that the difference in fishing power between nets of various mesh sizes may be a result of differences in the proportion of fish caught by each entanglement mode in each mesh size. They stated that the three modes of capture have different fishing powers that may vary with mesh size, but in general, wedging is more effective than gilling, and both these modes are much more effective than tangling. However, the results of our study show that for total fish numbers caught in all mesh sizes combined, most fish were gilled (60%), whereas wedged (17%) and tangled (23%) fish made up significantly lower proportions of the catch. This result suggests that, in the case of our study, gill nets do in fact "gill" fish rather than capture them by tangling or wedging.

Mesh-size selectivity was evident from the mean length of fish captured by each method in each mesh size. Although the fork length of gilled and wedged fish increased with increasing mesh size, the fork length of tangled fish was less uniform in its relationship with mesh size.

The results of our study show that tangling is not the result solely of size selection and is not consistent across mesh sizes. The proportions of *Odax pullus* caught by each method, when plotted against fork length, show a clear transition as fork length increases from most fish being wedged to the majority being tangled. This transition would not occur if the size of tangled fish were independent of mesh size, because fish of all sizes would then become tangled in any given mesh size.

Although the concept of gill net "saturation," or diminishing returns with increasing effort, is generally recognized as a limiting factor in catch per unit of time (Minns and Hurley, 1988), there have been relatively few studies directed at exploring the mechanisms that limit the catch. Our study shows evidence of a set-time saturation effect with all three mesh sizes. Neither the number of fish caught nor the number of species caught were significantly different between the six and fifteen hour sets. However, these different set times had only a small overlap diurnally and saturation may have been influenced by differing periods of fish activity. There was no evidence in either the gill nets or in both underwater observations and videos (Hickford and Schiel, unpubl. data) that predators affected catches.

Space limitation in the gill net itself is regarded as a major component of the saturation effect. Once a fish has been captured, the particular cell that it occupies and the cells immediately surrounding it are not capable of catching other fish. Koike and Takeuchi (1982) examined this feature and found that fish were repulsed around a captured individual for some but not all mesh sizes. Kennedy (1951) cited additional ways in which the efficiency of a gill net decreases with time. These included the presence of captured, struggling fish (which makes the net more obvious and could frighten other fish away) and the presence of dead fish (which may cause other fish to avoid the area). Kennedy speculated that the greater the catch during the initial time period, the greater the difference between the initial (observed) and final (expected) catches.

The effect of set time on total and species catches in gill nets has a direct bearing on the use of this gear in assessing the abundance and species diversity of fish populations. Some studies have focused on comparing multi- to one-night catches (Richards and Schnute, 1986; Minns and Hurley, 1988).The evidence presented here, however, suggests that net saturation can occur during a single night, although this may be confounded by the varying behaviors of the fish species present.

The apparent similarity in catch rates of *Odax pullus*, *Arripis trutta*, *Aplodactylus arctidens*, and *Latridopsis ciliaris* during day and night sets was unexpected. These species are more active during the day and would be expected to be caught in significantly greater numbers in the day sets. Greater average numbers of these species were caught during the daytime, but the catches were so variable that any patterns may have been masked.

The condition of fish in the landed catch is closely related to the length of time a net is in the water. The catch of nets set for longer than six hours will contain a high proportion of damaged fish. The relation between set time and condition is confounded by the fact that nets set for periods longer than six hours were usually left in the water overnight. Dur-

ing the hours of darkness, lobsters (*Jasus edwardsii*) feed more actively (Gunson, 1983) and can severely damage fish. However, lobsters often become tangled in nets while feeding on dead or dying fish in the bottom region of the nets and were frequently caught during nighttime sets in this study. Most intertidal and subtidal marine isopods also peak in their activity rates during the hours of darkness (Jones and Naylor, 1970; Fincham, 1973). Sea lice can completely devour all but the skin and calcified structures of a fish. The fact that both these predators feed predominantly at night means that damage incurred by fish would be greater for overnight sets.

In our study, few fish were damaged in the six hour sets, but up to 40% of fish were damaged in the fifteen hour sets. Therefore, any increase in the number of fish caught beyond six hours may be offset by more fish being severely damaged.

Gill nets do not representatively sample the fish population at reef sites; none of the species in this study was caught in its proportional occurrence in nearshore habitats (Hickford and Schiel, 1995). Behavioral traits, such as swimming motion, and morphological characteristics, such as spines or large fins, act to make some species more vulnerable than others to the fishing action of gill nets. The 2.5" mesh is clearly the most effective at catching most species of fish and is particularly effective at capturing juvenile and resident reef fish. Nets of this small mesh size are commonly available to amateur fishermen in New Zealand, who use them in nearshore waters. Our study clearly shows that although commercially valuable species, such as *Odax pullus, Latridopsis ciliaris,* and *Arripis trutta,* can be caught in great numbers around coastal reefs, the bycatch of resident species, such as *Aplodactylus arctidens, Notolabrus fucicola,* and a broad range of others, is considerable. Most of these species are of no commercial value, but their removal from nearshore waters may well have long-term consequences on resident fish populations in areas where considerable gill netting occurs, such as around the Kaikoura Peninsula.

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Kalman filtering the delay-difference equation: practical approaches and simulations

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Abstract.—Recently, J. J. Pella showed how the Kalman filter could be applied to production modeling to estimate the size and productivity of fish stocks from a time series of catches and relative abundance indices. We apply these methods to the Deriso-Schnute delay-difference equation. The Kalman filter approach incorporates process and measurement error naturally in the model description. When the production model is the delay-difference equation, the error structure is particularly attractive because process error can be interpreted as simply the variance of recruitment, and measurement error as the variance of the relative abundance estimates. We derived prior distributions of initial biomass in order to begin the Kalman filter calculations. Reanalysis of the data from the eastern tropical Pacific for yellowfin tuna, *Thunnus albacares*, shows that modeling results can differ greatly depending on whether error is interpreted to be process error or measurement error. Simulation results show that nonlinear least squares and Kalman filter estimates agree well if data contain only measurement error. In contrast, the Kalman filter was clearly superior if simulated data contained significant amounts of process error. The presence of process error positively biased biomass estimates from both the nonlinear least-squares and Kalman filter methods. The Kalman filter performed well with Schnute's form of the delay-difference equation, even though this model violates the assumption of independent process error vectors. The Kalman filter also performed well when the variance ratio r was assumed known and individual variances were estimated from the data. However, it appeared difficult to estimate r as a parameter in the maximum-likelihood estimation.

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Fishery production models are used to model fishery population dynamics when only catch (measured in biomass units) and relative abundance data are available. Originally, only fishery catch-per-unit-of-effort data (Schaefer, 1954; Pella and Tomlinson, 1969) were used as relative abundance indices for fish populations, but surveys often provide less biased abundance measures. Therefore, both time series of fishery CPUE and survey abundance indices are commonly used estimates of relative abundance.

Production models contrast with age-structured models, such as ADAPT (Gavaris, 1988) and Stock Synthesis (Methot, 1989), that model the population cohort in numbers at age and typically require catch-at-age data. Age-structured models allow for variation in recruitment which has given this class of model greater credence among stock assessment scientists. However, age data are technically difficult to obtain, expensive, and contain biases and variability that can be difficult to interpret. In addition, age-structured models often contain a large number of parameters, and sifting through possible solutions when fitting multiple sources of data can be subjective.

Because of these data requirements and technical problems, production models have remained of interest to stock assessment scientists. Recent production model offerings have included statistical refinements such as bootstrapping (Prager, 1994), Bayesian analysis (Hoenig et al., 1994), and the treatment of statistical error (Polachek et al., 1993). Two of the earliest papers to consider both process and measurement error in population dynamics modeling were those of Ludwig and Walters (1981) followed by Collie and Sissenwine (1983). The Kalman filter approach, which allows the consideration of both process and measurement error, now appears to be becoming standard for assessments by either production or age-structured models (Mendelssohn, 1988; Sullivan, 1992; Pella, 1993; Schnute, 1991, 1994).

The methods described in this paper meld two distinct pieces of technology: the delay-difference equation (Deriso, 1980; Schnute, 1985), and the Kalman filter (Kalman, 1960; Harvey, 1990; Pella, 1993). Collie and Walters (1991) used the Kalman filter to predict and update biomass estimates on the basis of the delay-difference equation but did not use the Kalman filter for parameter estimation. The delay-difference equation has deep roots in fishery modeling. In fact, to a remarkable extent it can encompass the fundamental paradigms of age structure, exponential

survival, and von Bertalanffy growth. The Kalman filter (Kalman, 1960), on the other hand, originated in engineering where it has been widely used in control theory and quality control. The basic idea of Kalman recursive filtering (Meinhold and Singpurwalla, 1983) is that the current state of the system (i.e. the current fish biomass) can be estimated from the system's past (biomass) estimates in two steps: a forecast step and an update step. The forecast estimate is made prior to the current observation of relative abundance; the updated estimate is made following the current observation of relative abundance. The updated estimate of biomass is the modeler's best estimate of the "true" biomass and is, roughly speaking, a weighted average between the forecast and observed abundance values. The updated biomass estimate is used to forecast the next biomass estimate, which then is updated with the next observed value. The absolute and relative magnitude of process and measurement error, which are assumed normal and whose values are generally assumed by the filter, largely determine the result of the update step. If there is little process error assumed by the filter, updating will not substantially change the forecast biomass estimate.

For fishery modeling, the most salient feature of the Kalman filter is its allowance for both process and measurement error. In the implementation of the delay-difference equation with the Kalman filter, process error can be interpreted as the variance of recruitment,[1] and measurement error as the variance of the estimate of relative abundance. Thus the Kalman filter method allows for variation in recruitment, a property that heretofore seemed to be exclusive to age-structured models.

The implementation of the Kalman filter presented here is due to Pella (1993), who applied the method to a simple recruitment model ascribed to Schnute (1991) and to the generalized production model of Pella and Tomlinson (1969). For comparative purposes, we also fitted the delay-difference equation with ordinary nonlinear least squares, which in this case assumes that data contain only measurement error.

The delay-difference population dynamics model

The delay-difference equation is a simple biomass-based model that contains the core dynamics of age-structured models (Deriso, 1980; Schnute, 1985). Thus under many conditions the population dynamics described by the delay-difference equation should agree with that of age-structured models (e.g. virtual population analysis). The applications of the delay-difference equation we propose require the following parameter values and information:

1 The instantaneous natural mortality rate M.
2 Brody[2] growth parameters ρ and ω.
3 Annual catches in biomass c_t, $t=1,...n$.
4 Annual survey biomass estimates y_t, either relative (catchability unknown) or absolute (catchability known) abundance indices, with a few missing values allowed.

The natural mortality rate, M, is always difficult to know but estimates or educated guesses are usually available. The Brody growth parameters can be estimated with nonlinear least squares on relatively small aged samples that provide weight-at-age data (Schnute, 1985):

$$W_{k+j} = \omega_{k-1} + (\omega_k - \omega_{k-1})(1-\rho^{1+j})/(1-\rho) \quad \text{for } j \geq 0. \tag{1}$$

Here, W_{k+j} is the observed weight of a $k+j$ yr-old fish, ω_{k-1}, ω_k, and ρ are parameters to be estimated, and k is the age at recruitment. Our application of the delay-difference equation requires $\omega = \omega_{k-1}/\omega_k$ so that $\hat{\omega} = \hat{\omega}_{k-1}/\hat{\omega}_k$. The difference between Deriso's and Schnute's forms of growth (and hence their delay-difference equations) is that Deriso's original equation requires unrealistically that $\omega_{k-1} = 0$ so that $\omega = 0$. A simple substitution in Schnute's more general formulations of growth and delay-difference equation results in Deriso's forms of growth and delay-difference equation.

Catches and fishing effort are usually among the first statistics collected from a fishery. Survey estimates of stock biomass sometimes come later through significant cost and effort by fisheries management agencies (Gunderson, 1993). If insufficient numbers of survey estimates are available, fishery CPUE can provide the biomass indices. However, fishery CPUE data may bias model estimates because catchability often changes over time. Survey data provide either relative (catchability unknown) or absolute (catchability known) biomass abundance indices. Absolute abundance estimates for a few years will typically

[1] A reviewer noted that process error can also arise from other factors, such as variability in growth and survival, and other sources that make the deterministic delay-difference population dynamics incorrect.

[2] A reviewer pointed out that "Ford" may be a better name for these growth parameters (Ricker, 1975).

constrain an analysis more accurately than will many years of relative abundance indices.

Population dynamics are described by Schnute's (1985, $\omega > 0$) or Deriso's (1980, $\omega = 0$) delay-difference equation:

$$B_t = (1+\rho)s_{t-1}B_{t-1} - \rho s_{t-1}s_{t-2}B_{t-2} + R_t - \rho\omega s_{t-1}R_{t-1}. \quad (2)$$

For the case when $t=2$,

$$B_2 = (1+\rho)s_1B_1 - \rho s_1s_0B_0 + R_2 - \rho\omega s_1R_1. \quad (3)$$

B_t and R_t are the population biomass and recruitment biomass at the beginning of year t, and s_t is total survival during year t (note B_t includes R_t).

The delay-difference equations allow for variable recruitment. In the data analysis and simulations performed in this paper the recruitment process is assumed to have constant mean, i.e. $E(R_t) = R_1$ for all t. The delay-difference Kalman filter method allows for variable recruitment by considering variable recruitment to be process error about the mean recruitment. The nonlinear least-squares estimation method allows only for measurement error, therefore the recruitment process is assumed to be strictly constant with $R_t = R_1$ for all t.

However, both the nonlinear least-squares and Kalman filter methods can be easily generalized to have mean recruitment as a function of stock biomass in earlier years. In this case $E(R_t) = f(B_{t-k})$, where $k \geq 1$ (Kimura, 1988).

Estimating parameters with nonlinear least squares

To fit the delay-difference equation with nonlinear least squares, we must provide biomass projections $\{B_t\}$, from Equations 2 and 3, using as parameters to be estimated, initial values (B_1, R_1). If B_1 is assumed to be virgin biomass and R_1 is in equilibrium with B_1, the expected (i.e. equilibrium) recruitment line (ERL) follows from Equation 2 (Kimura, 1985):

$$R_1 = B_1\{[1-\rho\exp(-M)][1-\exp(-M)]\}/[1-\rho\omega\exp(-M)]. \quad (4)$$

The ERL is a straight line through the origin of the (B_1, R_1) plane.

The initial parameters (B_1, R_1) may be parameterized by either of two assumptions: 1) B_1 is virgin biomass or 2) B_1 is not virgin biomass. If B_1 is virgin biomass, R_1 is determined from Equation 4 (or conversely, B_1 can be determined from R_1). B_2 can then be projected from Equation 3, with $B_0 = B_1$ and $s_0 = \exp(-M)$. Projections of biomass for $t>1$ requires $\{s_t, t = 1, ..., n\}$. These survivals $s_t = \exp(-M-F_t)$, are obtained by iteratively solving the catch equations for F_t (Kimura and Tagart, 1982):

$$c_t = B_tF_t(1-\exp(-M-F_t))/(M+F_t) \quad (5)$$

in a sequential manner (relative to t). If B_1 is not virgin biomass, B_1 and R_1 are independent parameters to be estimated. The initial projection value $B_0 = B_1$ will be used, but with $s_0 = \exp(-M-F_0)$ if information concerning F_0 is available. In either case, further projections of biomass can be made by using Equation 2.

In the simulations to be presented, we assume that the initial population is a virgin biomass (i.e. Equation 4 holds). This allows us to initiate the biomass time series using the results in Appendix 1 and to fit the simulated data without substantial model bias. However, the fits to the simulated data with both nonlinear least squares and the Kalman filter will *not* assume virgin biomass. Instead, the delay-difference equation is fit to a time series of relative abundance data by varying three parameters: B_1, R_1, and a catchability coefficient λ. We assume the catchability coefficient scales the biomass projections from the delay-difference equation $\{B_t\}$ to the expected values of observed relative abundance indices $\{y_t\}$ (i.e. $E(y_t) = \lambda B_t$). For nonlinear least squares, if abundance indices y_t have coefficient of variation cv_t, parameters can be estimated by minimizing

$$SS = \sum[\ln(y_t) - \ln(\lambda B_t)]^2 / cv_t^2. \quad (6)$$

We used a lognormal formulation because of its superior numerical stability in quasi-Newton estimation algorithms. Parameters were estimated in two stages: initial estimates were found by a direct search over a grid of values for B_1, R_1, then refined by using quasi-Newton methods.

The survey catchability λ can be either estimated or fixed depending on whether y_t is thought to be a relative or absolute index of abundance. Differentiating Equation 6 with respect to λ and solving the normal equation shows that λ can be estimated by

$$\hat{\lambda} = \exp\left\{\sum\left[\ln(y_t/\hat{B}_t)/cv_t^2\right]/\sum\left[1/cv_t^2\right]\right\} \quad (7)$$

so that at this stage searches for λ are not necessary. However, the final minimization of Equation 6 with quasi-Newton methods should be based on all three

parameters $\Psi = (\ln(B_1), \ln(R_1), \ln(\lambda))$, because the estimates by using Equation 7 may be suboptimal. If the coefficient of variation is the same for all y_t, then all cv_t can be set equal to one.

We also briefly examined the possibility of estimating nonlinear least-squares parameters by modeling both measurement and process error:

$$SS = \sum \left[(y_t - \hat{\lambda}\hat{B}_t)^2 / \sigma_m^2 + (R_t - \hat{R}_1)^2 / \sigma_p^2 \right]. \quad (8)$$

Here, $\hat{R}_1$ is the estimated mean recruitment as before, but R_t $t > 1$, are allowed to vary. For Deriso's form of the delay difference equation, differentiating Equation 8 with respect to R_t and setting the result equal to zero yields

$$\hat{R}_t = \left[(R_1 / r) + \lambda (y_t - \lambda P_t) \right] / \left[(1/r) + \lambda^2 \right], \quad (9)$$

where $r = \sigma_p^2 / \sigma_m^2$, and P_t is the delay-difference projection of biomass to year t prior to adding recruitment. Estimating parameters by minimizing Equation 8 appeared unstable and was not pursued further. This may be because mean recruitment R_1, and the individual recruitments R_t, both were estimated from the data. With additional constraints, or if recruitment indices were available, such an approach might be useful.

Maximum-likelihood estimation for the Kalman filter

We also applied the Kalman filter as described by Pella (1993) to the delay-difference equation. Pella (1993) credits Harvey (1990) for his own presentation, but we found Pella's presentation to be quite adequate for applying the method. As described earlier, the main reason for using the Kalman filter is that it allows for process error in addition to measurement error. The nonlinear least-squares estimates of the previous section assume constant recruitment and allow only for measurement error.

The state transition equation of the Kalman filter views the delay-difference equation (Eq. 2) as being composed of both deterministic and stochastic components. The determinisitic component of the process assumes that the expected values of R_t and R_{t-1} are constant, say equal to R_1. If desired, we can also assume virgin biomass when applying the Kalman filter, i.e. we can estimate R_1 by using Equation 4. This is analogous to the constant nonrandom recruitment model fit by nonlinear least squares. The biomass prediction given by Equation 2 is in error owing to variability in recruitment. This variability is defined to be process error. Now, even though B_t and λ have definite though unknown values, the abundance index y_t is observed only with error, which we define as measurement error. The Kalman filter method provides maximum-likelihood estimates of B_0, R_1, and λ, almost the same parameters as for the nonlinear least-squares method but for the process and measurement error model we have just described. Note that we estimate B_0 (see below) instead of B_1 because B_0 cannot simply be defined to be equal to B_1 in the equations which initialize the Kalman filter method. For consistency, when comparing parameter estimates for nonlinear least-squares and the Kalman filter methods, we shall compare only estimates of B_1 (i.e. the one year projection of B_0).

Modeling and assumptions in addition to those of nonlinear least squares are needed by the Kalman filter. Because the Kalman filter is essentially a Bayesian procedure (Meinhold and Singpurwalla, 1983), it requires a prior joint distribution for B_0 and B_{-1}. In addition, in order to partition process and measurement error, either the magnitude of process or measurement error (or both) or their ratio must be known or estimated. Nearly all of our simulations will assume that process and measurement error variances are known. Kalman filter estimation without prior information concerning error variances appears to be generally difficult.

Simulating datasets satisfying Kalman filter assumptions

In this section we describe simulation of relative abundance indices that satisfy the assumptions of the delay-difference equation and the Kalman filter. As stated earlier, these simulations assume virgin biomass (i.e. Equation 4 holds with B_0 substituted for B_1). This is the easiest way to avoid an initial modeling bias in the simulation and model fits. Data simulated in this manner will be fitted by using nonlinear least-squares and the delay-difference Kalman filter methods *without* the assumption of virgin biomass. To a large extent we followed the notation of Pella (1993). Note that the "state space" of the system is simply jargon for the unobservable true biomass of the system.

Initial conditions and assumptions The initial state of the system is defined to be

$$\alpha_0 = \begin{pmatrix} B_0 \\ B_{-1} \end{pmatrix}.$$

We assume that α_0 is unknown but has prior distribution with mean

$$a_0 = E(\alpha_0) = \begin{pmatrix} B_0 \\ B_0 \end{pmatrix}$$

and with covariance matrix

$$P_0 = \Sigma(\alpha_0) = \begin{pmatrix} \gamma_0 & \gamma_1 \\ \gamma_1 & \gamma_0 \end{pmatrix}.$$

Estimators for γ_0 and γ_1 are provided in Appendix 1 and only require prior estimates of ρ, ω, σ_p^2 and s_0. To predict α_1, we assumed

$$T_0 = \begin{pmatrix} (1+\rho)s_0 & -\rho s_0 s_0 \\ 1 & 0 \end{pmatrix}, C_0 = \begin{pmatrix} R_1(1-\rho\omega s_0) \\ 0 \end{pmatrix},$$

$$\tilde{R}_0 = \begin{pmatrix} 1 & -\rho\omega s_0 \\ 0 & 0 \end{pmatrix}, \text{and } \eta_0 = \begin{pmatrix} n_1 \\ n_0 \end{pmatrix}.$$

The state of the system at time t=1 is then $\alpha_1 = T_0\alpha_0 + C_0 + \tilde{R}_0\eta_0$, where n_1 is assumed to be a normal random variable with mean zero and variance σ_p^2. For Deriso's form of the delay-difference equation, $\omega = 0$, so that the value of n_0 is irrelevant. However, for Schnute's form of the delay-difference equation we used $n_0 = 0$ because the data contained no information concerning n_0.

Projecting the state space Given the initial conditions (above), and a catch sequence $\{c_t\}$, the state space variable α_t can be projected indefinitely:

$$\alpha_t = \begin{pmatrix} B_t \\ B_{t-1} \end{pmatrix}, T_t = \begin{pmatrix} (1+\rho)s_t & -\rho s_t s_{t-1} \\ 1 & 0 \end{pmatrix}, C_t = \begin{pmatrix} R_1(1-\rho\omega s_t) \\ 0 \end{pmatrix}$$

$$\tilde{R}_t = \begin{pmatrix} 1 & -\rho\omega s_t \\ 0 & 0 \end{pmatrix}, \eta_t = \begin{pmatrix} n_{t+1} \\ n_t \end{pmatrix}$$

so that

$$\alpha_{t+1} = T_t\alpha_t + C_t + \tilde{R}_t\eta_t.$$

The process error vectors η_t are assumed to be independent with

$$E(\eta_t) = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

and with covariance matrix

$$Q = \begin{pmatrix} \sigma_p^2 & 0 \\ 0 & \sigma_p^2 \end{pmatrix}.$$

Recall that T_t requires a value for s_t by first solving Equation 5 for F_t.

Addition of measurement error Given a catchability coefficient λ, the observed variables can be described as $y_t = Z\alpha_t + \varepsilon_t$, where $Z = (\lambda\ 0), \varepsilon_t = e_t$, and e_t is assumed to be normally distributed with mean zero and variance $h = \sigma_m^2$.

If expected recruitment is to be a function of stock biomass in earlier years, the state space project vector C_t must become a function of α_t so that

$$C_t(\alpha_t) = \begin{pmatrix} E(R_{t+1}) - \rho\omega s_t E(R_t) \\ 0 \end{pmatrix}.$$

If the delay between hatching and recruitment is to be many years, then the dimension of α_t must be increased, so that the earlier biomass will be available to calculate recruitment.

So far we have described a statistical model which includes process and measurement error and which can be used to compute a realization of relative abundance indices, say $\{\tilde{y}_t\}$. In the implementation of the Kalman filter given here, Deriso's form ($\omega = 0$) of the delay-difference equation fully satisfies the assumptions of the model, but Schnute's ($\omega > 0$) more realistic form does not. This difference is due to the process error vectors

$$\eta_t = \begin{pmatrix} n_{t+1} \\ n_t \end{pmatrix},$$

which represent variability in recruitment and which are assumed to be independent by the Kalman filter. Because η_t and η_{t+1} both contain n_{t+1}, this assumption is clearly violated for Schnute's form of the delay-difference equation. This trade-off between realism in the delay-difference equation and statistical independence required of process error will be examined further with simulation.

Kalman filter estimates

If values of variance for process and measurement error are assumed, parameters $\Psi = \{\ln(B_0), \ln(R_t), \ln(\lambda)\}$ can be estimated by the method of maximum likelihood. In principle, the method is very similar to that described for calculating nonlinear least-squares estimates. Given a value for Ψ, initial values for a_0, P_0 can be specified as in the simulations; estimates of biomass and its covariance matrix can then be forecast $\{a_{t|t-1}, P_{t|t-1}\}$. The value of Ψ, whose forecasts maximize the log-likelihood, is taken as the estimate.

Because the Kalman filter incorporates process as well as measurement error, estimation of biomass occurs in two steps.

1 Initial projections $a_{t|t-1} = T_{t-1}a_{t-1} + C_{t-1}$ and $P_{t|t-1} = T_{t-1}P_{t-1}T_{t-1}' + \tilde{R}_{t-1}Q\tilde{R}_{t-1}'$ are calculated on the

basis of the value of Ψ, initial conditions, and the data ($c_1, \ldots, c_{t-1}$)and ($y_1, \ldots y_{t-1}$). Recall again that T_{t-1} requires a value for s_{t-1} that can be estimated by first solving the catch equation (Eq. 5) for F_{t-1}. As described earlier, if expected recruitment is to be a function of earlier biomass estimates, then C_{t-1} must be a function of a_{t-1}.

2 If an observation of y_t exists, the initial projections $a_{t|t-1}$ and $P_{t|t-1}$ are updated on the basis of $a_t = a_{t|t-1} + P_{t|t-1}Z' f_t^{-1}(y_t - Za_{t|t-1})$ and $P_t = P_{t|t-1} - P_{t|t-1}Z' f_t^{-1} ZP_{t|t-1}$, where $f_t = ZP_{t|t-1}Z' + h$. If an observation of y_t does not exist, further projections can be made by using Equation 1, with $a_{t|t-1}$ and $P_{t|t-1}$ used in place of a_t and P_t. Therefore, Kalman filter estimation can accommodate missing relative abundance indices provided they are few in number.

3 The log-likelihood is calculated to be

$$\ln(L(y,\Psi)) = -\left(\frac{n}{2}\right)\ln(2\pi) - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t) - \frac{1}{2}\sum_{t=1}^{n}\frac{v_t^2}{f_t},$$

where $v_t = y_t - Za_{t|t-1}$, and $f_t = ZP_{t|t-1}Z' + h$.

As with the nonlinear least-squares method, the Kalman filter estimate of Ψ was also calculated in two stages. First, we searched a grid of possible initial λ_0 values, say from 0.5 to 1.5 at 0.1 intervals. For each fixed λ_0 value, we then estimated the conditional maximum-likelihood estimate $\Psi^* = [\ln(B_0^*), \ln(R_1^*)]$ by a quasi-Newton method. We then picked the λ_0^* and Ψ^* having the largest conditional likelihood, and used that as an initial estimate for finding the unconditional maximum likelihood estimate $\hat{\Psi} = [\ln(\hat{B}_0), \ln(\hat{R}_1), \ln(\hat{\lambda})]$, again by using a quasi-Newton method. The asymptotic covariance matrix of the maximum-likelihood estimates can be estimated from the inverse Hessian of minus the log-likelihood.

Generally, our Kalman filter estimates were made with the assumption that process and measurement error variances were known. However, under the Kalman filter, if $r = \sigma_p^2/\sigma_m^2$ is known, then all model parameters, including σ_m^2 and hence σ_p^2, can be estimated from the data. Following Pella (1993), we reparameterized $h = 1$ and

$$Q = \begin{pmatrix} r & 0 \\ 0 & r \end{pmatrix}.$$

It can be noted that

$$P_0^* = P_0/\sigma_m^2 = \frac{1}{\sigma_m^2}\begin{pmatrix} \gamma_0 & \gamma_1 \\ \gamma_1 & \gamma_0 \end{pmatrix} = rA,$$

where $A = P_0/\sigma_p^2$ is dependent only on ρ, ω, and s_0. The Kalman recursions are then carried forward just as would have been done if no reparametrization had been performed. However, the covariance matrices $\{P_{t|t-1}$ and $P_t\}$ are now automatically scaled versions $\{P_{t|t-1}^* = P_{t|t-1}/\sigma_m^2$ and $P_t^* = P_t/\sigma_m^2\}$, and $f_t^* = f_t/\sigma_m^2$. The vectors $a_{t|t-1}$ and a_t are unaffected by the scaling which cancels in their equations. The parameter estimates are dependent only on the value of r, not the variance components σ_p^2 and σ_m^2. However, σ_m^2 can be estimated from

$$\hat{\sigma}_m^2 = \sum(v_t^2/f_t^*)/n,$$

where n is the number of y_t observed (also $\hat{\sigma}_p^2 = r\hat{\sigma}_m^2$). The log-likelihood to be maximized (see Appendix 2) then becomes

$$\ln(L_c(y,\Psi)) = -\frac{n}{2}[\ln(2\pi)+1] - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t^*) - \frac{n}{2}\ln(\hat{\sigma}_m^2). \quad (10)$$

The question arises whether r can be estimated as just another parameter by using the method of maximum likelihood? Although estimation of r appears possible in theory, our experience suggests that this will be impractical for many data sets. The reason is that the likelihood function appears to be insensitive to r (Fig. 1).

Data analysis and simulations

We reanalyzed the data set for yellowfin tuna, *Thunnus albacares* (Table 1), taken from Pella and Tomlinson (1969) by using methods described in this paper. Ages read from otoliths of yellowfin tuna (Wild, 1986) indicate that length at age is nearly linear. This implies exponential growth in weight at age, but we shall assume linear growth in weight at age (i.e. $\rho = 1.0$, $\omega = 0.0$). Because fish rapidly disappear from the population at age 4 yr, we assume $M = 0.60$. Therefore, we assume constant growth with a large natural mortality rate. Analysis by Pella (1993) indicates a biomass range of from 600 to 1,400 million pounds and an annual sustainable yield of 193 million pounds.

Our data analyses (i.e. fits to the data in Table 1) assume

D1 $\sigma_m^2 = 46, \sigma_p^2 = 32{,}775$ as reported by Pella (1993). These values suggest that most of the error

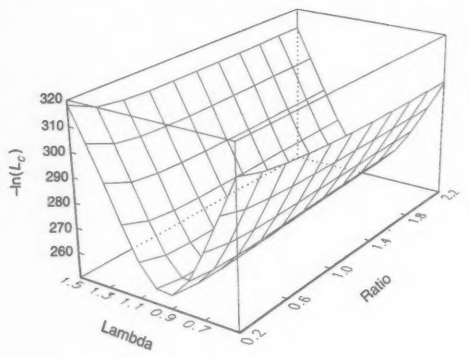

Figure 1

The likelihood profile (minus $\ln(L_c)$) for estimating Kalman filter parameters as a function of the variance ratio ($r = \sigma_p^2/\sigma_m^2$) and lambda ($\lambda$), showing that the likelihood profile appeared insensitive to the value of variance ratio. The assumed parameters were $R_1 = 250$, $\lambda = 1$, $\rho = 1$, $\omega = 0$, $M = 0.60$, $s_0 = \exp(-0.60)$, r=1.0, variances assumed to be $\sigma_m^2 = 100$ $\sigma_p^2 = 100$, with n = 100 yr of simulated data.

is process error (i.e. variance of recruitment) as opposed to measurement error (i.e. error in measuring the relative abundance index).

D2 $\sigma_m^2 = 5{,}000$ $\sigma_p^2 = 1{,}000$. These values suggest that most of the error is measurement error as opposed to process error.

Under the heading "Simulating datasets satisfying Kalman filter assumptions," we describe a detailed model for simulating data that satisfy the Kalman filter assumptions. In this paper all simulations are roughly related to the yellowfin tuna dataset (i.e. 34 yr of simulated data with similar model parameter values). To do this we specified values for natural mortality, M, Brody growth parameters ρ and ω, expected recruitment R_1, catchability λ, and variances σ_p^2 and σ_m^2. Assuming virgin biomass (Eq. 4), values for $(M, \rho, \omega, \sigma_p^2, R_1)$ provide us with the mean virgin biomass and its covariance matrix over neighboring years (a_0, P_0). The simulation is initialized by generating biomass estimates, i.e. bivariate normal random deviates having the prior expectation a_0 and covariance matrix P_0. These initializations assumed $s_0 = \exp(-M)$. Because trends in the catch data can affect modeling results, we also simulated the catch data by assuming that catches were lognormal (see Kimura, 1989), $\ln(c_t) \sim N(\mu, \sigma^2)$, with $E(c_t) = \bar{c}$, and $\text{var}(c_t) = cv^2\bar{c}^2$, with $\bar{c} = 141.8$ (average from Table 1), and $cv = 0.2$.

Table 1

Catch (c_t in million pounds) and relative abundance (y_t in pounds per boat day) for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean (Pella and Tomlinson, 1969).

Year	Catch	Relative abundance
1934	60.9	10,361
1935	72.3	11,484
1936	78.4	11,571
1937	91.5	11,116
1938	78.3	11,463
1939	110.4	10,528
1940	114.6	10,609
1941	76.8	8,018
1942	42.0	7,040
1943	50.1	8,441
1944	64.9	10,019
1945	89.2	9,512
1946	129.7	9,292
1947	160.2	7,857
1948	207.0	8,353
1949	200.1	8,363
1950	224.8	7,057
1951	186.0	10,108
1952	195.3	5,606
1953	140.0	3,852
1954	140.0	5,339
1955	140.9	8,191
1956	177.0	6,507
1957	163.0	6,090
1958	148.5	4,768
1959	140.5	4,982
1960	244.3	6,817
1961	230.9	5,544
1962	174.1	4,120
1963	145.5	4,368
1964	203.9	4,844
1965	180.1	4,166
1966	182.3	4,513
1967	178.9	5,292

Three simulations were replicated 100 times so that we could examine the bias, variance, and root mean square error (i.e. the square root of mean square error) of Kalman filter and nonlinear least-squares parameter estimates when the true parameter values were known. For these simulations we assumed that the stock was initially a virgin biomass ($R_1 = 250$, $\lambda = 1$, $\rho = 1$, $\omega = 0$, $M = 0.60$), and the catch data were generated as lognormal random deviates $LN(\bar{c}=141.8, cv = 0.2)$. We assumed that data sets had only measurement error, only process error, or a mixture of both.

S1 $\sigma_m^2 = 1{,}000$ $\sigma_p^2 = 1$. Measurement error only.

S2 $\sigma_m^2 = 1$ $\sigma_p^2 = 1{,}000$. Process error only.

S3 $\sigma_m^2 = 500$ $\sigma_p^2 = 500$. Measurement and process error.

In order to understand the distribution of bias in the estimated biomass trends, we made histograms of the residuals $Z_t = \hat{B}_t - B_t$ (true) for years t=1, 17, and 34, for both the Kalman filter and nonlinear least-squares estimates.

Finally, two specialized simulations were replicated 100 times:

SP1

$\omega > 0$:

$$R_1 = 250,\ \lambda = 1,\ \rho = 0.75,\ \omega = 0.75,$$
$$M = 0.3,\ \sigma_m^2 = 1,\ \sigma_p^2 = 1{,}000$$

SP2

r fixed:

$$R_1 = 250,\ \lambda = 1,\ \rho = 1,\ \omega = 0,$$
$$M = 0.6,\ \sigma_m^2 = 500,\ \sigma_p^2 = 500.$$

With these simulations the stock was assumed to be initially a virgin biomass. The purpose of simulation SP1 was to examine how severely the correlation in process error (η_t) induced by Schnute's form of the delay-difference equation ($\omega > 0$) degrades the parameter estimates from the Kalman filter. The purpose of SP2 was to examine whether estimating parameters by assuming only $r = \sigma_p^2 / \sigma_m^2 = 1.0$ was known (i.e. by maximizing Equation 10), would degrade the Kalman filter estimates.

Results

Our results from reanalyzing the data set in Table 1 with variance assumptions described as D1 and D2 are shown in Figure 2. The variance assumption D1, that of Pella (1993), is close to assuming only process error. The result is estimated biomass trends that are scaled but that exactly trace the relative abundance indices (Fig. 2A). Our model fit is very similar to that reported by Pella (1993) and indicates that, despite great differences in the underlying state transition models (delay-difference versus generalized production), the Kalman filter method, with large process error, can provide quite similar estimates of biomass trends. The nonlinear least-squares fit assumes only measurement error and differs considerably from the Kalman filter fit. In the analysis with variance assumed to be D2, the Kalman filter assumes that error is predominantly measurement error but also contains a realistic component of process error. The result is Kalman filter estimates of relative abundance that are very similar to nonlinear least-squares estimates (Fig. 2B).

Results from replicated simulations based on assumptions S1–S3 are shown in Table 2. Under the variance assumption S1, we have only measurement error. Under this assumption, the Kalman filter and nonlinear least-squares methods performed similarly. Root mean square error (RMSE) estimates, compared with sample standard deviations of parameter estimates, show that both methods have little bias but that the inverse Hessian of minus the log-likelihood appears to give estimates of the uncertainty of parameter estimates that are biased low (i.e. are more similar to standard deviation than RMSE). Residual plots (Fig. 3) indicate biomass traces have symmetrical error.

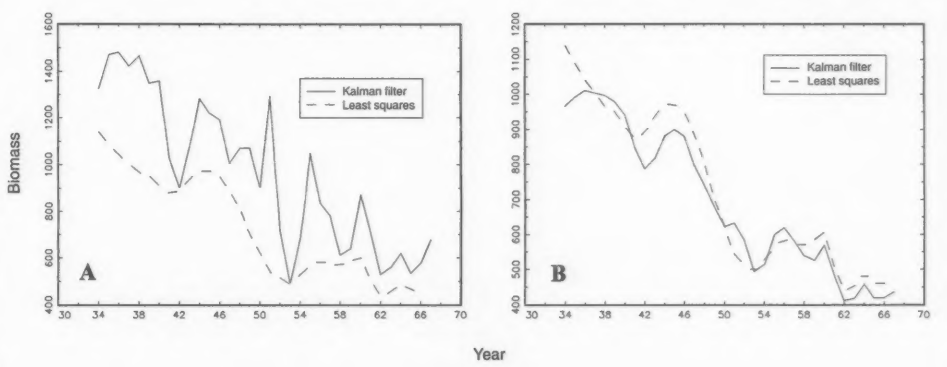

Figure 2

Fits to yellowfin tuna, *Thunnus albacares*, assuming $\rho = 1$, $\omega = 0$, $M = 0.60$, $s_0 = \exp(-0.60)$, and data from the eastern Pacific Ocean (Table1). (**A**) Kalman filter fit assuming $\sigma_m^2 = 46$ $\sigma_p^2 = 32{,}775$ as in Pella (1993). (**B**) Kalman filter by assuming predominantly measurement error $\sigma_m^2 = 5{,}000$ $\sigma_p^2 = 1{,}000$. Nonlinear least-squares estimates are the same in both (A) and (B); biomass is in millions of pounds.

Table 2

Simulation result from 100 replications of the simulations described below. Time series were simulated by assuming virgin biomass with (R_1=250, λ=1), growth parameters (ρ=1, ω=0), s_0=exp(–0.60), σ_m^2,σ_p^2 values given below, and relationships described in Appendix 1. Catches were simulated as lognormal random variables with $\bar{c}$=141.8, cv=0.2). Because the true B_1 value varies in each replication, an average value for each simulation is presented below. Standard errors for Kalman filter (KF) estimates were calculated from the inverse of the Hessian of minus the log-likelihood. RMSE = root mean square error; NLS = nonlinear least squares.

	B_1	R_1	λ
Simulation S1: $\sigma_m^2 = 1{,}000$ $\sigma_p^2 = 1$			
Average true B_1	1,228		
Average of Kalman filter estimates	1,237	250.9	1.004
Standard deviation of KF estimates	135	13.3	0.098
Average standard error of KF estimates	175	16.4	0.120
RMSE of KF estimates	232	23.0	0.169
Average NLS estimates	1,235	250.7	1.007
Standard deviation of NLS estimates	140	14.1	0.106
RMSE of NLS estimates	240	24.3	0.183
Simulation S2: $\sigma_m^2 = 1$ $\sigma_p^2 = 1{,}000$			
Average true B_1	1,222		
Average of Kalman filter estimates	1,282	256.9	0.963
Standard deviation of KF estimates	139	15.5	0.095
Average standard error of KF estimates	154	14.8	0.094
RMSE of KF estimates	244	29.2	0.176
Average NLS estimates	1,332	263.7	1.082
Standard deviation of NLS estimates	618	67.6	0.431
RMSE of NLS estimates	1,072	118.9	0.756
Simulation S3: $\sigma_m^2 = 500$ $\sigma_p^2 = 500$			
Average true B_1	1,230		
Average of Kalman filter estimates	1,287	257.0	0.979
Standard deviation of KF estimates	232	24.5	0.153
Average standard error of KF estimates	228	22.0	0.145
RMSE of KF estimates	400	44.0	0.266
Average NLS estimates	1,304	259.4	1.026
Standard deviation of NLS estimates	481	52.8	0.263
RMSE of NLS estimates	831	92.4	0.455

With variance assumption S2, we have only process error. With this assumption both the Kalman filter and nonlinear least-squares biomass estimates are biased high (Table 2; Fig. 4). However, root mean square errors show that the Kalman filter performance is clearly superior to nonlinear least squares for this case. It is interesting that simulation S2 also shows that nonlinear least-squares estimates are not necessarily more biased under process error but that parameter estimates have larger variances.

Variance assumption S3 represents a combination of process and measurement error. Results from S3 are similar to those from S2, with biomass estimates appearing to be biased high for both the Kalman filter and nonlinear least-squares methods (Table 2; Fig. 5), but with RMSE clearly favoring the Kalman filter method over the nonlinear least-squares method. It should be noted that in simulation S2 and S3, 1 or 2 of the nonlinear least-squares fits failed to converge probably owing to the inclusion of process error. These simulations were thrown out and the runs were repeated.

Results from simulation SP1 (Table 3) indicate that Schnute's form of the delay-difference equation can be used with the Kalman filter, despite the violation of the assumption that process error vectors are independent. And finally, results from simulation SP2 (Table 4) indicate that the Kalman filter parameter estimates have smaller RMSE compared with nonlinear least-squares parameter estimates when only the value of $r = \sigma_p^2 / \sigma_m^2$ is assumed in the model fit.

Conclusions

Simulations show that with the fit of the delay-difference equation, the Kalman filter and nonlinear least-

squares methods give similar results if there is only measurement error. Bias in parameter estimates for both methods tend to be small in this case. The Kalman filter was superior to nonlinear least squares, as measured by RMSE, if there is only process error. Both methods tended to give biomass estimates that were positively biased, and nonlinear least-squares estimates were dramatically skewed to the right. A similar result

Table 3

Simulation result from 100 replications of the simulation described as SP1 in the text. Time series were simulated by assuming virgin biomass (R_1=250, λ=1), growth parameters (ρ=0.75, ω=0.75), s_0=exp (–0.30), (σ_m^2=1,σ_p^2=1,000), and relationships described in Appendix 1. Catches were simulated as lognormal random variables with ($\bar{c}$=141.8, cv=0.2). Because the true B_1 value varies in each replication, an average value for each simulation is presented below. Standard errors for Kalman filter (KF) estimates were calculated from the inverse of the Hessian of minus the log-likelihood. RMSE = root mean square error.

	B_1	R_1	λ
Simulation SP1: $\sigma_m^2 = 1, \sigma_p^2 = 1{,}000$			
Average true B_1	1,262		
Average of Kalman filter estimates	1,287	252.1	0.993
Standard deviation of KF estimates	155	16.4	0.113
Average standard error of KF estimates	159	16.2	0.105
RMSE of KF estimates	257	28.5	0.195

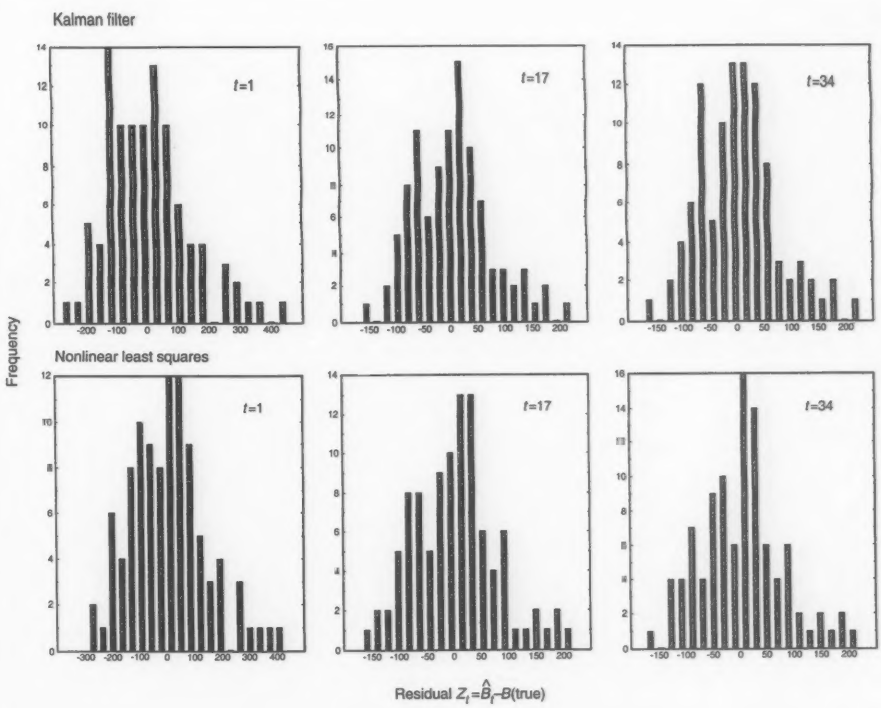

Figure 3

Histograms of the residual between estimated and true biomass, $Z_t = \hat{B}_t - B_t$(true), for simulation S1, with $\sigma_m^2 = 1{,}000$, and $\sigma_p^2 = 1.0$. Top row is for the Kalman filter method; bottom row is for the nonlinear least-squares method; columns are for years t=1, 17, and 34.

occurred when measurement and process error were included in the simulations, the Kalman filter and nonlinear least-squares biomass estimates were positively biased and appeared positively skewed.

We interpret these results to mean that the Kalman filter method provides superior performance in terms of RMSE but provides biased biomass estimates. This is a serious problem for a stock assess-

Table 4

Simulation result from 100 replications of the simulation described as SP2 in the text. Time series were simulated by assuming virgin biomass (R_1=250, λ=1), growth parameters (ρ=1, ω =0), s_0=exp(–0.60), $\sigma_m^2 = 500$ $\sigma_p^2 = 500$, and relationships described in Appendix 1. Catches were simulated as lognormal random variables with ($\bar{c}$=141.8, cv=0.2). Because the true B_1 value varies in each replication, an average value for each simulation is presented below. KF = Kalman filter; RMSE = root mean square of error; NLS = nonlinear least squares.

	B_1	R_1	λ
Simulation SP2: $\sigma_m^2 = 500$ $\sigma_p^2 = 500$			
Average true B_1	1,226		
Average of Kalman filter estimates	1318	259.9	0.967
Standard deviation of KF estimates	291	28.6	0.173
RMSE of KF estimates	502	55.6	0.313
Average NLS estimates	1310	260.3	1.035
Standard deviation of NLS estimates	565	61.7	0.290
RMSE of NLS estimates	982	107.8	0.503

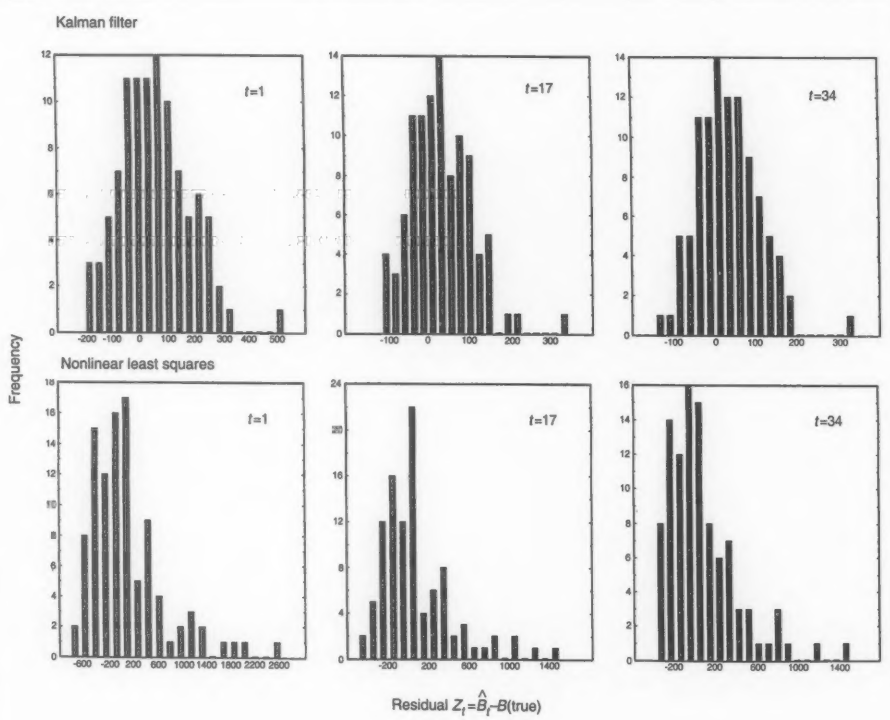

Figure 4

Histograms of the residual between estimated and true biomass, $Z_t = \hat{B}_t - B_t$(true), for simulation S2, with $\sigma_m^2 = 1.0$, and $\sigma_p^2 = 1{,}000$. Top row is for the Kalman filter method; bottom row is for the nonlinear least-squares method; columns are for years t=1, 17, and 34.

ment model because it can lead to overfishing. However, simulation results also indicate that under the presence of process error, nonlinear least-squares methods provide biomass estimates with comparable bias, and have much poorer RMSE properties. We therefore conclude that the Kalman filter method provides superior parameter estimates in the face of process error.

Simulation results indicate that Schnute's form of the delay-difference equation can be used with the Kalman filter despite violation of the independent process error assumption. Although it appears difficult to estimate r directly with maximum-likelihood estimation, simulation results indicate that the Kalman filter can be used to estimate biomass when only $r = \sigma_p^2 / \sigma_m^2$ is known, rather than the individual variances.

It is important to acknowledge that simulation results will differ if natural mortality, catch levels, growth parameters, biomass, and recruitment, or error variances, are changed. We believe that customized simulation studies should be a routine part of production modeling. The simulations performed in this paper favored the Kalman filter in that the true measurement and process error variances were assumed to be known to the Kalman filter fitting algorithm. Under these circumstances, the performance of the Kalman filter method might be described as less than fully satisfactory.

There appears to be few published simulation studies describing the performance of production models in the presence of process error. Process error is particularly troublesome because errors are propagated through the years rather than being quickly forgotten as is measurement error. Our results, and those of Polacheck et al. (1993), indicate that parameter estimation in the presence of process error is inherently difficult for production models. However, the process error method of Polacheck et al. (1993) is regression-based and may not provide fully efficient parameter estimates. Because real data contain process error, we feel process error must be dealt with,

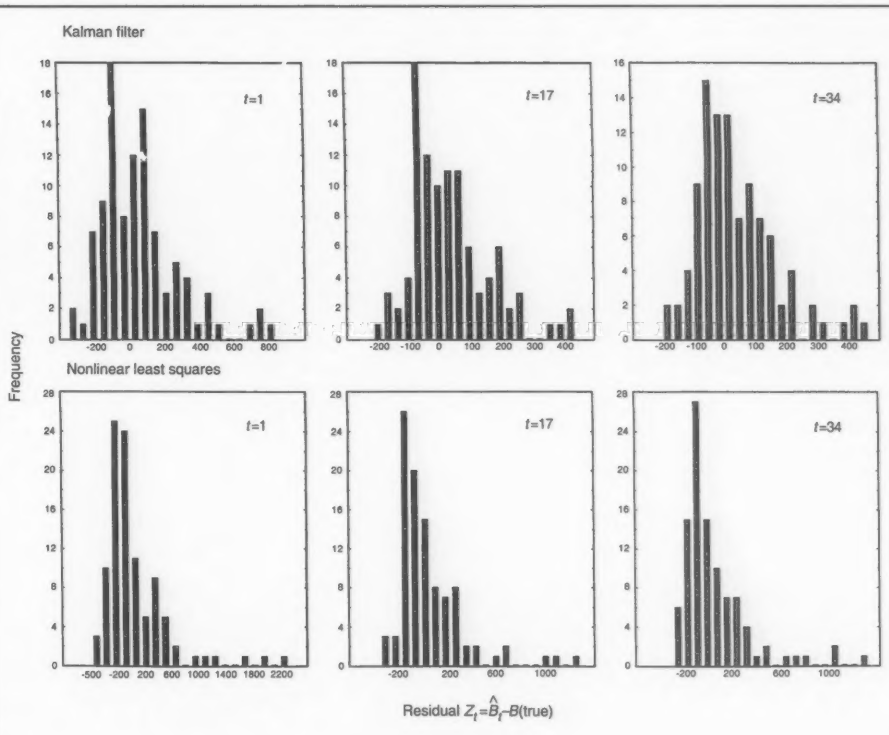

Figure 5

Histograms of the residual between estimated and true biomass, $Z_t = \hat{B}_t - B_t$ (true), for simulation S3, with $\sigma_m^2 = 500$, and $\sigma_p^2 = 500$. Top row is for the Kalman filter method; bottom row is for the nonlinear least-squares method; columns are for years t=1, 17, and 34.

at least to the extent of investigating the effects of such errors on modeling results.

One final note. In this paper we have not emphasized model output beyond biomass traces and basic parameter estimates. For example, annual estimates of fishing mortality rates and exploitation rates were obvious byproducts of the model fits we presented. The models presented here can be thought of as extensions to what we earlier called Stock Reduction Analysis (Kimura and Tagart, 1982; Kimura et al., 1984; Kimura 1985, 1988). These papers contain various methods of analysis that are useful for providing fishery management advice. For example, output from both the Kalman filter and nonlinear least-squares models can be treated as a constant recruitment model, and target ABC's (allowable biological catches) or target biomass levels can be made on the basis of this assumption.

Acknowledgments

This paper was inspired by J. J. Pella's lucid application of the Kalman filter method (Pella, 1993). We thank J. J. Pella for reviewing the manuscript, and providing numerous corrections, clarifications, and improvements. Also, we thank two anonymous reviewers for helpful comments and corrections.

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Appendix 1: Time series properties of the delay-difference equation

If recruitments $\{R_t\}$ are assumed to be uncorrelated with $E(R_t) = R_1$ and $V(R_t) = \sigma_p^2$, then the delay-difference equation (Eq. 2) is close to being a standard ARMA time series model (Box and Jenkins, 1970). Let $\phi_1 = (1+\rho)s_0, \phi_2 = -\rho s_0^2$, and $\theta = \rho\omega s_0$. Then Equation 2 can be written as

$$B_t = \phi_1 B_{t-1} + \phi_2 B_{t-2} + R_t - \theta R_{t-1}. \quad (1')$$

Defining $B_1 = (R_1 - \theta R_1)/(1-\phi_1-\phi_2)$, and substituting $R_t = n_t + R_1$ and $B_t = \tilde{B}_t + B_1$ into Equation 1', yields the process

$$\tilde{B}_t = \phi_1 \tilde{B}_{t-1} + \phi_2 \tilde{B}_{t-2} + n_t - \theta n_{t-1}, \quad (2')$$

where n_t the are now white noise. Thus under the assumption of constant growth parameters (ρ, ω), constant survival s_0, and random recruitment (R_t), the displaced process $\{\tilde{B}_t\}$ is an ARMA time series model with the same statistical properties of $\{B_t\}$.

The stationarity and invertibility of this time series can easily be established by considering the roots of the characteristic polynomials (see Box and Jenkins, 1970):

$$1 - \phi_1 X - \phi_2 X^2 = 0, \text{ and} \quad (3')$$

$$1 - \theta X = 0. \quad (4')$$

The stationarity and invertibility of $\{\tilde{B}_t\}$ follows from the observation that the roots $1/s_0$ and $1/(\rho s_0)$ of Equation 3' and $1/(\rho\omega s_0)$ of Equation 4' are all almost surely greater than unity.

Let $c_0 = (1-\theta\phi_1+\theta^2)\sigma_p^2$, and $c_1 = -\theta\sigma_p^2$. The autocovariance terms (i.e. the γ_k in standard notation) of the process $\{B_t\}$can then be shown to be

$$\gamma_0 = [c_0 + (1+\phi_2)\phi_1 c_1/(1-\phi_2)]/[(1-\phi_2^2) - (1+\phi_2)\phi_1^2/(1-\phi_2)],$$
$$\gamma_1 = (c_1 + \phi_1\gamma_0)/(1-\phi_2),$$
$$\gamma_2 = \phi_1\gamma_1 + \phi_2\gamma_0, \text{ and}$$
$$\gamma_k = \phi_1\gamma_{k-1} + \phi_2\gamma_{k-2}, \text{ for } k \geq 3.$$

Two interesting correlation coefficients that can be estimated using the γ_k are

$$\rho(B_t, R_t) = \sqrt{\sigma_r^2/\gamma_0} \text{ and } \rho(B_{t-k}, B_t) = \gamma_k/\gamma_0.$$

Appendix 2: Derivation of the log-likelihood when only the variance ratio $r = \sigma_p^2/\sigma_m^2$ is known.

Source: Pella, J. J. 1995. Auke Bay Laboratory, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau, AK 99801. Personal communication.

We start with the usual log-likelihood when variances are assumed known

$$\ln(L(y,\Psi)) = -\frac{n}{2}\ln(2\pi) - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t) - \frac{1}{2}\sum_{t=1}^{n}\frac{v_t^2}{f_t}. \quad (1'')$$

Substituting $f_t = \sigma_m^2 f_t^*$ into (1"), we have

$$\ln(L(y,\Psi)) = -\frac{n}{2}\ln(2\pi) - \frac{n}{2}\ln(\sigma_m^2) - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t^*) - \frac{1}{2\sigma_m^2}\sum_{t=1}^{n}\frac{v_t^2}{f_t^*}. \quad (2'')$$

By differentiating with respect to σ_m^2, and by setting this result equal to zero, we obtain the estimator

$$\hat{\sigma}_m^2 = \frac{1}{n}\sum_{t=1}^{n}\frac{v_t^2}{f_t^*},$$

which we substitute into Equation 2" to arrive at the function to be maximized

$$\ln(L_c(y,\Psi)) = -\frac{n}{2}[\ln(2\pi)+1] - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t^*) - \frac{n}{2}\ln(\hat{\sigma}_m^2). \quad (3'')$$

Genetic variation and phylogenetic relationships of seven oreo species (Teleostei, Oreosomatidae) inferred from allozyme analysis

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Abstract.—Fishing pressure on deepwater oreosomatids has increased recently in Australian and New Zealand waters, and yet little is known about these fish. Genetic variation and phylogenetic relationships among Australian species was examined. Allozyme variation at 26 loci was examined in seven species: six from Australasia (*Allocyttus niger*, black oreo; *A. verrucosus*, warty oreo; *Neocyttus rhomboidalis*, spiky oreo; *Oreosoma atlanticum*, oxeye oreo; *Pseudocyttus maculatus*, smooth oreo; and a new species *Neocyttus* sp., rough oreo, infrequently captured with the smooth oreo and black oreo) and one from the North Atlantic (*N. helgae*). Two phenetic trees were constructed: an unweighted pair-group method with arithmetic averaging (UPGMA) tree derived from Nei's unbiased genetic distances and a distance-Wagner tree derived from Rogers' distances. A maximum parsimony cladistic analysis, with loci as characters and alleles as unordered states, was also performed. Outgroup species came from three related families: Acanthuridae, Berycidae, and Zeidae.

Mean heterozygosity per locus for the seven oreo species was relatively high for teleosts (11.8%), with *O. atlanticum* having the lowest value (8.3%) and *N.* sp. having the highest value (18.1%). *Oreosoma atlanticum* was the most divergent, with a mean genetic identity (I) of 0.371. The two most closely related species—*N. rhomboidalis* and *N. helgae* (I=0.973)—did not have any diagnostic allozyme loci, although the muscle protein patterns, after Coomassie blue staining, were distinctive. There was little evidence to support the inclusion of *A. niger* and *A. verrucosus* in the same genus; these two species had a genetic identity of 0.695. *Allocyttus niger* appeared to be more closely related to members of the genus *Neocyttus* than to *A. verrucosus*. Phenetic analyses revealed only minor differences in the Oreosomatidae grouping with respect to the three outgroups, whereas cladistic analyses revealed the Zeidae as the most closely related family.

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Oreos are laterally compressed, deep-bodied fish with large heads and large eyes. They are found in deepwater (below 500 m) over the continental slopes of most temperate, and some tropical and subtropical, regions. They appear to be more common in the Southern Hemisphere, but this may reflect a greater deepwater trawling effort in such regions as New Zealand and Australia.

The family Oreosomatidae (order Zeiformes) contains four genera. In a revision of oreos from the southern oceans, James et al. (1988) reported that, although the family is well defined and recognizable, its generic relationships are less clear: the genera *Allocyttus*, *Neocyttus*, and *Oreosoma* need redefining. The fourth genus, *Pseudocyttus*, is well defined and distinguishable.

Oreos are among the most abundant benthopelagic fishes on the continental slope of southern Australia, yet little is known of their biology, stock structure, or phylogeny. In New Zealand waters, oreos have been fished commercially since the late 1970's. A peak catch of 26,500 metric tons (t) was taken in 1981–82; the fishery has since moderated to around 19,000 t per year (Lyle et al., 1992). The New Zealand fishery comprises two main species: the smooth oreo (*Pseudocyttus maculatus* Gilchrist, 1906) and the black oreo (*Allocyttus niger* James et al., 1988). In Australian waters oreos have been caught largely as a bycatch of the deepwater fisheries for blue grenadier (*Macruronus novaezelandiae* (Hector, 1871)) and orange roughy (*Hoplostethus atlanticus* Collett, 1889) and were generally discarded. However, recent drastic reductions in orange roughy catch limits, the development of new deepwater fishing grounds off southern Tasmania, and growing market awareness have resulted in increased targeting of species aggregations and a rapid growth and retention of Australian catches of oreos (Lyle et al., 1992). The retained catch of oreo from the southeast fishery (the main deepwater trawl fishery in Australia) was less than 100 metric tons (t) per annum before 1987, around 2,000 t in 1990 and 1991, over 3,000 t in 1992, and over 1,000 t in 1993 and 1994 (Australian Fisheries Management Authority[1]). Actual catches are prob-

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[1] Australian Fisheries Management Authority. 1995. Burns Centre, 28 National Circuit, Forrest Act 2603, Australia. Unpubl. data.

ably higher because some are not reported and others discarded (Lyle et al., 1992). The recorded tonnages of individual species are unreliable owing to confusion over species identification in the catch log books. As in New Zealand, the smooth and black oreos dominate the Australian catch, whereas the spiky oreo (*Neocyttus rhomboidalis* Gilchrist, 1906) and the warty oreo (*Allocyttus verrucosus* (Gilchrist, 1906)) are also important. A fifth species, the oxeye oreo (*Oreosoma atlanticum* Cuvier, 1829), is commonly caught but discarded because of its small size and low commercial value.

This paper presents the results of an allozyme survey of the five described Australasian species (*Allocyttus niger*, *A. verrucosus*, *Neocyttus rhomboidalis*, *Oreosoma atlanticum*, and *Pseudocyttus maculatus*) and a new species (the rough oreo, *Neocyttus* sp., Yearsley and Last[2]) often captured with *A. niger* and *P. maculatus*. A third *Neocyttus* species, *N. helgae* (Holt and Byrne, 1908), from the North Atlantic, was also examined.

Oreosomatids not included in this study are the North Pacific *Allocyttus folletti* Myers, 1960, the southern Atlantic and Indian Ocean *Allocyttus guineensis* Trunov and Kukuev in Trunov, 1982, and the Indian Ocean *Neocyttus acanthorhyncus* (Regan, 1908). Another member of the family, the Southern Ocean *Pseudocyttus nemotoi* (Abe, 1957), was recently resurrected by Miller (1993).

The intrarelationships of zeiforms have not been discussed in the literature; thus outgroup selection for this phylogenetic study is difficult. Many authors consider the beryciforms to be more primitive than the zeiforms but closely related to them (e.g. Greenwood et al., 1966). Zehren (1979) found the Berycidae to be more primitive than the remaining beryciform families and, thus, a berycid may be a suitable outgroup. However, Rosen (1984) dramatically changed the placement of the zeiforms, including them in the order Tetraodontiformes, with the Caproidae as the sister group to all other tetraodontiforms (the caproids' placement within the Zeiformes was questioned by others [Tighe and Keene, 1984]). A caproid may therefore be a suitable outgroup. Furthermore, Rosen placed the zeids immediately before the oreosomatids in his new division Zeomorphi. He used "acanthurids plus chaetodontids" to establish character polarities. Consequently, a zeid or an acanthurid are also possible outgroups. In the absence of caproid specimens, three outgroups were selected for analysis: the berycid *Beryx splendens* Lowe, 1833 (alfonsino), the zeid *Cyttus australis* (Richardson, 1843) (silver dory), and the acanthurid *Naso tuberosus* Lacepède, 1802 (humphead unicornfish).

Genetic variation present in the Australasian oreosomatids and diagnostic allozyme loci for each species are presented in this paper to assist in future management plans for the developing deepwater fishery. The phylogenetic relationships of previously known species, as well as a new species from Australia and a species from the North Atlantic, are discussed in an effort to understand more fully the systematics of the family Oreosomatidae.

Materials and methods

Samples of muscle and liver tissue were collected from seven oreosomatids (*Allocyttus niger*, *Allocyttus verrucosus*, *Neocyttus* sp. (voucher specimen: CSIRO H2865.01), *Neocyttus helgae*, *Neocyttus rhomboidalis*, *Oreosoma atlanticum* and *Pseudocyttus maculatus*), and from the three outgroup species (*Beryx splendens*, *Cyttus australis*, and *Naso tuberosus*). Sample details and species abbreviations are given in Table 1.

Whole fish were frozen after capture and transported frozen to the laboratory, where tissues were dissected and held at –80°C. Small pieces of tissue were placed in 1.5-mL microcentrifuge tubes, homogenized manually with a few drops of distilled water, and spun at 11,000 rpm in a microcentrifuge for 2 minutes. The supernatant was used for electrophoresis.

Allozyme variation was examined with three gel systems: gel system A—Helena Titan III cellulose acetate plates run at 200 V with a Tris-glycine buffer (0.020 M tris and 0.192 M glycine, Hebert and Beaton[3]); gel system B—Helena Titan III cellulose acetate plates run at 150 V with a Tris-citrate buffer (0.075 M tris and 0.025 M citric acid, pH 7.0); gel system C—8% Connaught starch gels with a histidine/citrate buffer (gel buffer: 0.005 M histidine HCl, pH 7.0; electrode buffer: 0.41 M trisodium citrate, pH 7.0). Standard staining procedures were followed (Richardson et al., 1986; Hebert and Beaton[3]).

In all, 19 enzymes, representing 27 loci, were examined (Table 2) and allele frequencies determined (Table 3). However, the locus *GPI-A** was not included in the phylogenetic analyses because of poor resolution in three species (*A. niger*, *N.* sp., and *P. maculatus*). Loci and alleles are designated by the nomenclature system outlined in Shaklee et al. (1990), except that peptidase loci were identified as *PEP1** and

[2] Yearsley, G. K., and P. R. Last. 1995. CSIRO Division of Fisheries, Castray Esplanade, Hobart, Tasmania 7000, Australia.

[3] Hebert, P. D. N., and M. J. Beaton. 1989. Methodologies for allozyme analysis using cellulose acetate electrophoresis: a practical handbook. Helena Laboratories, Beaumont, Texas.

Table 1

Collection details for specimens analyzed in this study and species abbreviations adopted in this paper.

Species	Abbrev.	Collection area	No. of fish	Collection date
Allocytus niger	AN	Tasmania	202	May 1993
		South Tasman Rise	41	January/June 1992
		New Zealand	100	January 1994
			Total = 343	
Allocytus verrucosus	AV	Western Australia	336	January 1991/March 1992/August 1993
		Great Australian Bight	134	March–June 1992
		Tasmania	126	February 1992/November 1992/April 1994
		New South Wales	32	April 1994
		Lord Howe Rise	83	June 1992
		South Africa	11	September 1993
			Total = 722	
Neocyttus sp.	NA	Southern Tasmania	Total = 16	May 1993
Neocyttus helgae	NH	North Atlantic (ca. 61°39'N, 13°11'W)	Total = 35	February 1993
Neocyttus rhomboidalis	NR	Western Australia	145	October 1993
		Great Australian Bight	31	March 1992
		South Australia	114	October 1993
		Tasmania	451	May 1993–April 1994
		New South Wales	59	February/April 1994
		Lord Howe Rise	98	August 1993
		New Zealand	101	January 1994
			Total = 999	
Oreosoma atlanticum	OA	Southern Tasmania	19	October 1994
		Great Australian Bight	6	March 1992
			Total = 25	
Pseudocyttus maculatus	PM	Western Australia	99	October 1993
		Tasmania	200	May 1993
		New Zealand	100	January 1994
			Total = 399	
Beryx splendens	BS	Western Australia	Total = 6	June 1992
Cyttus australis	CA	Gabo Island, Bass Strait	Total = 6	September 1994
Naso tuberosus	NT	Queensland	Total = 2	March 1994

*PEP2**. Multiple loci encoding the same enzyme were designated by consecutive numbers, with '1' denoting the fastest migrating system. Alleles within each locus were identified by the anodal electrophoretic mobility (rounded to nearest 5%, except for *FH*113*) of their product relative to that of the most common allele observed in the spiky oreo, *N. rhomboidalis*, which was designated '100' (cathodal migration being designated negative). In addition, muscle protein patterns were examined after Coomassie Blue staining. These results are not included in the phylogenetic analyses because of uncertain homologies between species, but patterns were species-specific. The *CK-A** product was one of several protein products visualized by this general protein stain. The mean sample sizes per locus for the seven oreo species had a wide range (from 14 to 598, Table 4) because polymorphic loci for the four main commercial species (*A. niger*, *A. verrucosus*, *N. rhomboidalis*, and *P. maculatus*) were examined in large numbers for stock delineation studies (unpubl. data).

Species relationships were analyzed with BIOSYS-1 software (Swofford and Selander, 1981) and PAUP (phylogenetic analysis using parsimony) 3.0s soft-

Table 2

Details of enzymes used in this study. EC = Enzyme Committee; Tissue: l = liver, m = muscle; Gel: A = cellulose acetate with a Tris-glycine buffer, B = cellulose acetate with a Tris-citrate buffer, C = starch (see text). Multiple loci encoding for the same enzyme are designated by consecutive numbers, with '1' denoting the fastest migrating system. # = loci not included in analyses (see text).

Enzyme	EC number	Locus abbrev.	Locus no.	Tissue	Gel
Aspartate aminotransferase	2.6.1.1	*sAAT-1**	1	m	A
		*sAAT-2**	2	l	A
		*mAAT**	3	m/l	A
Alcohol dehydrogenase	1.1.1.1	*ADH**	4	l	A
Adenylate kinase	2.7.4.3	*AK**	5	m	B
Creatine kinase	2.7.3.2	*CK-A**	6	m	A
Esterase-D (UV, umb. acetate)	3.1.-.-	*ESTD**	7	m/l	A
Fumarate hydratase	4.2.1.2	*FH**	8	m	A
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	9	m	B
		*GAPDH-2**	10	m	B
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A**	#	m	A
		*GPI-B**	11	m	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-2**	12	m	B/C
Isocitrate dehydrogenase	1.1.1.42	*sIDHP**	13	m	C
		*mIDHP**	14	l	B
l-Lactate dehydrogenase	1.1.1.27	*LDH-C**	15	l	A
		*LDH-1**	16	l	A
		*LDH-2**	17	m	A
Malate dehydrogenase	1.1.1.37	*sMDH-1**	18	m	C
		*sMDH-2**	19	m	C
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	20	l	A
Peptidase (l-leucyl-l-tyrosine)	3.4.-.-	*PEP1-1**	21	l	A
Peptidase (leu-leu-leu)	3.4.-.-	*PEP2**	22	l	A
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	23	m	B/C
Phosphoglucomutase	5.4.2.2	*PGM-1**	24	l	A
		*PGM-2**	25	m/l	A
Superoxide dismutase	1.15.1.1	*sSOD**	26	l	A
General protein		*PROT*	#	m	A

ware (Swofford, 1991). Two phenetic methods of analysis of genetic distance obtained from the allele frequency data were examined with BIOSYS-1. First, Nei's (1978) unbiased genetic distance measure between each species was calculated, and trees were constructed by cluster analysis and the unweighted pair-group method with arithmetic averaging (UPGMA). Second, Rogers' (1972) distance measures were calculated and trees constructed by the distance-Wagner procedure (Farris, 1972) with outgroup rooting. The Wagner procedure, unlike the UPGMA analysis, does not assume a constant rate of evolution. For the cladistic maximum-parsimony analysis (PAUP), the loci were coded as characters and the most common alleles as unordered character states. When two common alleles were at equal frequencies (0.5), they were treated as multiple states and interpreted in the analysis as a polymorphism. The "branch and bound" and "exhaustive" routines were applied to search for the most parsimonious tree.

Results

Several measures of genetic variation were examined (Table 4). Four of the seven oreo species had average sample sizes per locus exceeding 200, but the average sample size for three species was less than 30. Two of the genetic variation parameters, mean number of alleles per locus and percentage of variable loci, are clearly dependent on sample size: both will increase as increasingly rare alleles are detected. Percentage of polymorphic loci, especially with use of the 0.95 rather than 0.99 criterion, will be less sample-size dependent, and mean heterozygosity per locus is little affected by rare alleles. In fact, estimates of heterozygosity (and genetic distance) are influenced more by numbers of loci than by numbers of individuals (Nei, 1978; Gorman and Renzi, 1979), and all estimates of heterozygosity given here are based on the same 26 loci. All oreos showed high levels of variation, with average

Table 3

Allele frequencies. Alleles are presented as allozyme electrophoretic mobilities relative to the most common allele recorded from spiky oreo (NR), *Neocyttus rhomboidalis*. Locus details are presented in Table 2 and species abbreviations are presented in Table 1. *n* = number of individuals scored, — = allele not detected, # = locus not scored due to poor resolution.

			Oreosomatids							Outgroup		
Locus		Allele	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
1	*sAAT-1**	115	—	—	—	—	—	1.000	—	—	—	—
		110	—	1.000	0.192	0.121	0.246	—	—	—	—	—
		100	1.000	—	0.808	0.879	0.754	—	0.962	—	—	—
		80	—	—	—	—	—	—	0.038	—	—	—
		75	—	—	—	—	—	—	—	—	1.00	—
		65	—	—	—	—	—	—	—	1.00	—	—
		35	—	—	—	—	—	—	—	—	—	1.00
		n	24	24	13	33	778	21	395	6	6	2
2	*sAAT-2**	125	—	—	0.125	0.014	0.001	—	—		—	
		120	—	—	—	—	0.001	—	—		—	
		100	1.000	0.994	0.875	0.986	0.996	—	0.988		—	
		90	—	—	—	—	—	1.000	—		—	
		80	—	0.003	—	—	0.002	—	0.008		0.83	
		60	—	0.003	—	—	—	—	0.004		—	
		55	—	—	—	—	—	—	—		0.17	
		n	226	178	16	35	422	21	248	#	6	#
3	*mAAT**	100	—	—	—	—	0.001	—	—	—	—	—
		0	—	—	—	—	0.007	—	—	—	—	—
		–100	1.000	1.000	0.962	0.958	0.884	1.000	0.959	—	—	—
		–110	—	—	—	—	—	—	—	—	—	1.00
		–150	—	—	—	—	—	—	—	1.00	—	—
		–200	—	—	0.038	0.042	0.107	—	0.041	—	1.00	—
		–250	—	—	—	—	<0.001	—	—	—	—	—
		n	226	178	13	36	971	25	413	6	6	2
4	*ADH**	125	—	—	—	—	—	—	1.000	—	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	—	—	—	—
		35	—	—	—	—	—	0.024	—	—	—	—
		30	—	—	—	—	—	—	—	1.00	—	—
		10	—	—	—	—	—	0.976	—	—	1.00	—
		–30	—	—	—	—	—	—	—	—	—	1.00
		n	226	178	16	35	422	21	248	6	6	2
5	*AK**	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	—	1.00
		80	—	—	—	—	—	—	—	—	1.00	—
		n	226	24	13	23	24	25	248	6	6	2
6	*CK-A**	110	—	0.845	0.269	—	<0.001	—	—	—	—	—
		100	0.872	0.155	0.731	1.000	0.952	1.000	—	—	—	—
		90	0.128	—	—	—	0.047	—	1.000	—	—	—
		80	—	—	—	—	<0.001	—	—	—	—	—
		75	—	—	—	—	—	—	—	—	—	1.00
		60	—	—	—	—	—	—	—	1.00	—	—
		50	—	—	—	—	—	—	—	—	1.00	—
		n	337	700	13	35	987	25	248	6	6	2
7	*ESTD**	135	—	—	—	—	—	—	—	—	1.00	—
		120	—	—	—	—	—	—	—	1.00	—	—
		115	1.000	1.000	0.846	—	—	—	1.000	—	—	1.00
		100	—	—	0.154	1.000	0.998	1.000	—	—	—	—
		85	—	—	—	—	0.002	—	—	—	—	—
		n	226	178	13	23	422	22	248	4	2	2

Table 3 (continued)

Locus		Allele	Oreosomatids							Outgroup		
			AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
8	*FH**	120	0.003	—	—	—	—	—	—	—	—	—
		115	—	0.002	—	—	—	—	0.007	—	—	—
		113	—	—	—	—	0.006	—	—	—	—	—
		110	—	—	—	0.030	—	—	0.027	—	—	—
		100	0.990	0.747	0.962	0.940	0.982	—	0.838	—	—	—
		95	—	—	—	—	—	—	—	—	—	1.00
		80	0.007	0.247	0.038	0.030	0.011	1.000	0.128	1.00	—	—
		65	—	0.004	—	—	—	—	—	—	1.00	—
		n	294	672	13	33	935	23	413	6	6	2
9	*GAPDH-1**	105	—	—	—	—	—	—	—	1.00	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	1.000	—	1.00	—
		90	—	—	—	—	—	1.000	—	—	—	1.00
		n	24	24	13	23	24	22	24	6	6	2
10	*GAPDH-2**	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	—	—	—
		75	—	—	—	—	—	—	—	1.00	1.00	—
		30	—	—	—	—	—	—	—	—	—	1.00
		n	24	24	16	23	24	25	24	6	6	2
11	*GPI-B**	140	—	0.001	—	—	0.004	—	—	—	—	—
		125	—	—	—	—	—	—	—	0.50	—	0.50
		120	—	0.071	—	—	—	—	—	—	—	—
		115	—	—	—	0.030	—	—	—	—	—	—
		110	—	—	—	—	—	—	—	0.42	—	0.50
		100	1.000	0.584	0.692	0.849	0.550	1.000	1.000	—	—	—
		95	—	—	—	—	—	—	—	0.08	—	—
		85	—	—	—	—	—	—	—	—	0.33	—
		80	—	0.343	0.269	0.121	0.446	—	—	—	—	—
		65	—	—	—	—	—	—	—	—	0.67	—
		60	—	0.001	0.039	—	<0.001	—	—	—	—	—
		n	226	694	13	33	983	25	248	6	6	2
12	*G3PDH-2**	165	—	—	—	—	0.002	—	—	—	—	—
		160	—	—	—	0.080	—	—	—	—	—	—
		145	—	—	—	—	—	1.000	—	—	—	—
		130	0.118	0.007	—	—	0.052	—	—	—	—	—
		100	0.561	0.526	0.846	0.355	0.900	—	—	—	—	—
		75	0.321	0.459	0.154	0.565	0.046	—	—	1.00	—	—
		70	—	—	—	—	—	—	1.000	—	—	—
		65	—	0.008	—	—	—	—	—	—	—	—
		25	—	—	—	—	—	—	—	—	1.00	—
		15	—	—	—	—	—	—	—	—	—	1.00
		n	279	291	13	31	918	18	248	6	6	2
13	*sIDHP**	120	—	—	—	—	—	1.000	—	—	—	—
		110	—	—	—	—	—	—	—	—	1.00	—
		105	—	—	—	—	—	—	—	1.00	—	—
		100	1.000	1.000	1.000	1.000	0.998	—	1.000	—	—	—
		65	—	—	—	—	—	—	—	—	—	1.00
		50	—	—	—	—	0.002	—	—	—	—	—
		n	226	178	13	18	494	21	248	6	6	2
14	*mIDHP**	105	—	—	—	—	—	1.000	—	—	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	1.000	—	—	—
		95	—	—	—	—	—	—	—	0.33	0.08	—
		85	—	—	—	—	—	—	—	0.42	0.92	1.00
		75	—	—	—	—	—	—	—	0.25	—	—
		n	226	178	15	22	422	24	248	6	6	2

Table 3 (continued)

Locus		Allele	Oreosomatids							Outgroup		
			AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
15	*LDH-C**	100	1.000	1.000	1.000	1.000	0.994	—	0.802	—	0.90	
		85	—	—	—	—	0.006	1.000	0.198	—	0.10	
		80	—	—	—	—	—	—	—	1.00	—	
		n	226	178	16	35	494	24	413	4	5	#
16	*LDH-1**	100	1.000	1.000	0.594	1.000	0.999	—	0.776	—	—	—
		40	—	—	0.406	—	0.001	—	0.224	1.00	—	—
		–15	—	—	—	—	—	1.000	—	—	1.00	—
		–35	—	—	—	—	—	—	—	—	—	1.00
		n	226	178	16	35	422	25	415	6	6	2
17	*LDH-2**	100	0.052	1.000	1.000	1.000	1.000	1.000	1.000	1.00	—	—
		50	0.948	—	—	—	—	—	—	—	—	—
		30	—	—	—	—	—	—	—	—	—	1.00
		–35	—	—	—	—	—	—	—	—	1.00	—
		n	336	178	13	23	422	25	248	6	6	2
18	*sMDH-1**	130	—	—	—	—	—	—	—	1.00	—	—
		125	—	—	—	—	—	1.000	—	—	—	—
		110	—	1.000	—	—	—	—	—	—	—	1.00
		100	1.000	—	1.000	1.000	1.000	—	1.000	—	—	—
		50	—	—	—	—	—	—	—	—	1.00	—
		n	226	178	13	23	422	22	248	6	6	2
19	*sMDH-2**	160	—	—	—	—	—	1.000	—	—	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	1.000	—	1.00	—
		95	—	—	—	—	—	—	—	—	—	1.00
		80	—	—	—	—	—	—	—	1.00	—	—
		n	226	178	16	23	422	25	248	6	6	2
20	*MPI**	110	—	0.219	—	0.071	0.049	—	—		—	—
		100	—	0.765	0.318	0.804	0.779	0.476	0.122		—	1.00
		90	1.000	0.016	0.682	0.125	0.170	0.524	0.878		1.00	—
		80	—	—	—	—	0.002	—	—		—	—
		n	226	276	11	28	903	21	388	#	6	2
21	*PEP1-1**	100	1.000	1.000	1.000	1.000	1.000	1.000	—	1.00	—	—
		90	—	—	—	—	—	—	0.998	—	—	—
		85	—	—	—	—	—	—	—	—	1.00	—
		80	—	—	—	—	—	—	0.002	—	—	1.00
		n	226	178	13	23	422	25	248	6	6	2
22	*PEP2**	105	—	1.000	—	—	—	—	—		—	
		100	1.000	—	1.000	1.000	0.999	1.000	0.507		—	
		85	—	—	—	—	0.001	—	0.493		—	
		80	—	—	—	—	—	—	—		1.00	
		n	226	24	13	23	422	21	402	#	6	#
23	*PGDH**	160	—	—	0.750	—	—	—	—	—	—	—
		150	—	—	0.208	—	—	—	—	—	—	—
		130	—	—	0.042	—	<0.001	—	—	—	—	—
		120	—	—	—	—	0.005	—	—	—	—	—
		115	—	—	—	—	—	1.000	—	—	—	—
		110	0.644	—	—	—	0.184	—	—	—	—	—
		105	—	—	—	—	—	—	—	1.00	—	—
		100	0.286	1.000	—	1.000	0.803	—	0.934	—	0.83	—
		90	—	—	—	—	0.007	—	0.033	—	0.17	—

Table 3 (continued)

Locus		Allele	Oreosomatids							Outgroup		
			AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
		85	—	—	—	—	—	—	0.033	—	—	—
		75	0.070	—	—	—	—	—	—	—	—	—
		60	—	—	—	—	—	—	—	—	—	1.00
		n	287	178	13	31	916	14	412	6	6	2
24	*PGM-1**	115	—	—	—	—	<0.001	—	—		—	—
		110	—	—	—	—	0.004	—	—		—	—
		105	—	0.137	—	—	0.099	—	—		—	—
		100	0.011	0.624	—	0.517	0.609	—	—		0.08	—
		95	0.696	0.222	0.433	0.450	0.242	—	0.017		0.83	—
		90	0.273	0.017	0.500	0.033	0.043	—	0.623		0.08	—
		85	0.020	—	0.067	—	0.003	0.250	0.025		—	—
		80	—	—	—	—	—	0.500	0.335		—	—
		75	—	—	—	—	—	0.250	—		—	1.00
		n	276	259	15	30	911	2	395	#	6	2
25	*PGM-2**	130	—	0.005	—	—	—	—	—	—	—	—
		125	—	—	—	—	0.002	—	—	—	—	—
		120	0.006	0.220	0.077	0.043	0.029	0.060	0.002	—	—	—
		100	0.591	0.749	0.923	0.943	0.925	0.840	0.874	—	—	—
		95	—	—	—	—	—	—	—	1.00	—	—
		80	0.282	0.016	—	0.014	0.040	0.060	0.123	—	—	—
		65	0.111	0.009	—	—	0.004	0.040	—	—	—	—
		60	—	—	—	—	—	—	—	—	1.00	—
		50	0.011	—	—	—	—	—	—	—	—	—
		40	—	—	—	—	—	—	—	—	—	0.75
		20	—	—	—	—	—	—	—	—	—	0.25
		n	330	676	13	35	972	25	414	6	6	2
26	*SOD**	180	—	—	—	0.014	—	0.021	0.374	—	—	—
		140	0.204	1.000	0.500	0.057	0.487	0.333	0.626	—	—	—
		130	—	—	—	—	—	—	—	—	1.00	—
		100	0.796	—	0.500	0.929	0.513	—	—	—	—	—
		60	—	—	—	—	—	0.646	—	1.00	—	—
		0	—	—	—	—	—	—	—	—	—	1.00
		n	329	178	19	35	983	24	412	6	6	2
Locus not included in analyses (see text):												
*GPI-A**		150		0.012		—	—	—		—	—	—
		140		0.002		—	—	—		—	—	—
		130		0.203		0.016	0.007	—		—	—	—
		125		0.005		—	0.014	—		—	—	—
		115		0.753		0.031	0.338	—		—		—
		110		—		0.484	—	—		—	—	—
		100		0.017		0.469	0.610	1.000		—	—	—
		95		0.007		—	—	—		—	—	—
		90		0.002		—	0.014	—		—	—	—
		85		—		—	0.016	—		—	—	—
		75		—		—	0.001	—		—	—	—
		45		—		—	—	—		1.00	—	—
		20		—		—	—	—		—	—	1.00
		10		—		—	—	—		—	1.00	—
		N	#	711	#	32	987	25	#	6	6	6

Table 4

Comparison of genetic statistical information for 26 loci scored in each oreosomatid species. A locus is considered variable when more than one allele is present, and polymorphic when the frequency of the most common allele is 0.95 or less. Mean and standard errors are presented. Mean heterozygosity per locus is Nei's (1978) unbiased estimate. Species abbreviations are defined in Table 1.

Species	Mean sample size per locus	Mean no. alleles per locus	Percentage of loci		Mean heterozygosity
			Variable	Polymorphic	
AN	228.1 ±16.7	1.6 ±0.2	30.8	26.9	0.105 ±0.038
AV	237.7 ±40.9	1.8 ±0.3	30.8	26.9	0.116 ±0.039
NA	14.0 ±0.3	1.7 ±0.1	53.8	46.2	0.181 ±0.041
NH	28.7 ±1.1	1.7 ±0.2	38.5	30.8	0.093 ±0.032
NR	597.6 ±63.1	2.5 ±0.3	65.4	34.6	0.127 ±0.037
OA	22.0 ±1.0	1.3 ±0.2	19.2	15.4	0.083 ±0.041
PM	297.8 ±22.0	1.8 ±0.2	50.0	34.6	0.121 ±0.034

heterozygosities ranging from 0.083 in *O. atlanticum* to 0.181 in *N.* sp.: the four commercial species (*A. niger*, *A. verrucosus*, *N. rhomboidalis*, and *P. maculatus*) had values ranging from 0.105 to 0.127. Despite the lowest mean sample size, *N.* sp. showed the highest proportion of polymorphic loci (46.2%) and the highest average heterozygosity.

Oreosoma atlanticum was the most divergent of the oreosomatids (Table 5). Its average genetic identity (Nei, 1978) (0 indicates complete dissimilarity and 1 complete similarity) with the other species was 0.371 (range 0.313 to 0.426 for 26 loci). The two most similar species were *N. rhomboidalis* and *N. helgae*, with a high genetic identity of 0.973. The third *Neocyttus* species, *N.* sp., had a relatively lower identity with the other two *Neocyttus* species: 0.903 with *N. rhomboidalis* and 0.884 with *N. helgae*. The two *Allocyttus* species had a genetic identity of only 0.695.

The three outgroup species were very divergent from both the oreosomatids and each other (Table 5). The acanthurid *N. tuberosus* diverged most from the oreosomatids, with an average genetic identity of 0.112 (range 0.085 to 0.180, from 23 loci). *Cyttus australis* had a mean identity with the oreosomatids of 0.171 (range 0.108 to 0.199, 26 loci) and *B. splendens* a mean identity of 0.164 (range 0.115 to 0.222, 22 loci).

In the acanthurid *N. tuberosus*, 16 of the 23 scorable loci were diagnostic (no shared alleles with any oreosomatid); in the zeid *C. australis*, 15 of 26 loci; and in the berycid *B. splendens*, 15 of 22 loci were diagnostic (Table 3). In a comparison of oreosomatids with one another, *O. atlanticum* had eleven diagnostic loci, *P. maculatus*, three, *A. verrucosus*, two, whereas the other four species revealed that only the muscle protein patterns were diagnostic (Table 3; Fig. 1). However, when the seven oreosomatids were compared pair-wise, each pair (except *N. rhomboidalis* with either *N.* sp. or *N. helgae*) had at least one and up to fourteen diagnostic allozyme loci, other than the general protein difference (Table 6). With the addition of between 4 and 13 loci showing significant allele frequency differentiation ($P<0.05$, with Bonferroni adjustment for multiple tests) (Table 6), even the closely related *N. rhomboidalis* and *N. helgae* were found to differ at five loci (*FH**, *GPI-A**, *GPI-B**, *G3PDH-2**, and *sSOD**) and *N. rhomboidalis* and *N.* sp. at eight loci (*sAAT-2**, *CK-A**, *ESTD**, *GPI-B**, *LDH-1**, *MPI**, *PGDH**, and *PGM-1**). The locus *PGDH** was diagnostic between *N.* sp. and *N. helgae*, with significant allele frequency differences at a further seven loci (*CK-A**, *ESTD**, *G3PDH-2**, *LDH-1**, *MPI**, *PGM-1**, and *sSOD**). *Oreosoma atlanticum* differed from

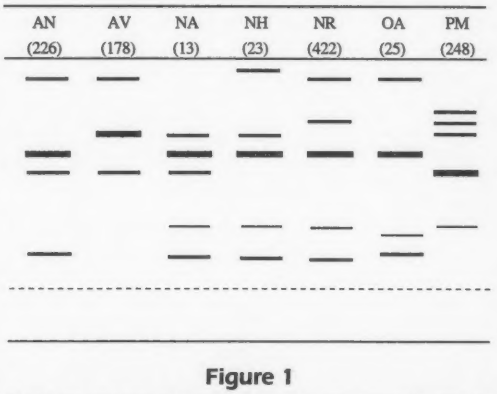

Figure 1

Banding pattern observed for each oreosomatid species with a general protein Coomassie blue stain (*PROT**). Dashed line indicates sample origin. Boldest band represents most common *CK-A** product in each species. Species abbreviations are defined in Table 1. Numbers in parentheses are number of individuals scored.

Table 5

Pairwise comparison of Nei's (1978) unbiased genetic identity (above diagonal) and genetic distance (below diagonal) between species for 26 loci, except for BS (22 loci) and NT (23 loci). Species abbreviations are defined in Table 1.

Species	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
AN	—	0.695	0.903	0.852	0.841	0.342	0.738	0.118	0.199	0.095
AV	0.364	—	0.773	0.761	0.788	0.313	0.659	0.183	0.169	0.180
NA	0.102	0.257	—	0.884	0.903	0.402	0.764	0.184	0.177	0.108
NH	0.160	0.273	0.123	—	0.973	0.426	0.711	0.174	0.180	0.085
NR	0.173	0.238	0.102	0.027	—	0.422	0.711	0.152	0.174	0.086
OA	1.073	1.161	0.913	0.853	0.864	—	0.319	0.222	0.108	0.128
PM	0.304	0.417	0.269	0.341	0.342	1.143	—	0.115	0.191	0.100
BS	2.138	1.700	1.694	1.749	1.885	1.505	2.159	—	0.068	0.095[1]
CA	1.614	1.780	1.734	1.714	1.748	2.227	1.653	2.689	—	0.042
NT	2.353	1.714	2.229	2.465	2.456	2.057	2.303	2.355[1]	3.168	—

[1] 21 loci common to both species.

the other six species at 17 to 22 loci, in addition to the general protein difference.

Two loci—*AK** and *GAPDH-2**—were invariant across all seven oreosomatid species, but only *GAPDH-2** differed in all three outgroup species; *AK** was different only in *C. australis*. These loci are consistent with a monophyletic origin of the oreosomatids. Three loci (*GAPDH-1**, *mIDHP**, and *sMDH-2**) were monomorphic for the same allele in six of the seven oreo species, with *O. atlanticum* fixed for alternative alleles; these putative synapomorphies indicate that these six species are probably monophyletic.

It is therefore not surprising to find that *O. atlanticum* was clearly separated from the other oreosomatid species on the phenogram constructed by the UPGMA method from Nei's (1978) unbiased genetic distances (Fig. 2). Branching order and significance of the branching nodes did not differ with the choice of outgroup. The three *Neocyttus* species and *A. niger* formed a distinct cluster. There was a very close association of the Southern Hemisphere *N. rhomboidalis* and the Northern Hemisphere *N. helgae*.

The phylogenetic tree constructed by the distance-Wagner procedure from Rogers' (1972) distances, rooted by the outgroup *C. australis*, also showed the divergence of *O. atlanticum* from the other oreosomatids (Fig. 3). Although the closeness of *N. rhomboidalis* and *N. helgae* was maintained, and again the two *Allocyttus* species were not grouped together, *P. maculatus* was found to be grouped with *A. niger* and *N.* sp. A similar tree was produced, by this procedure, with *N. tuberosus* as the outgroup, whereas the tree produced with *B. splendens* as the outgroup resembled those from the UPGMA cluster analyses (with *P. maculatus* divergent from the *Neocyttus* and *Allocyttus* species); a similar tree was produced when all three outgroups were applied together.

Cladistic analysis (PAUP) with all three outgroup species together produced 55 most parsimonious trees, all of which showed the divergence of *O. atlanticum* from other members of the family, but failed to define any structure for the other six species. Analysis with *C. australis* as the outgroup produced eleven most parsimonious trees of 52 units in

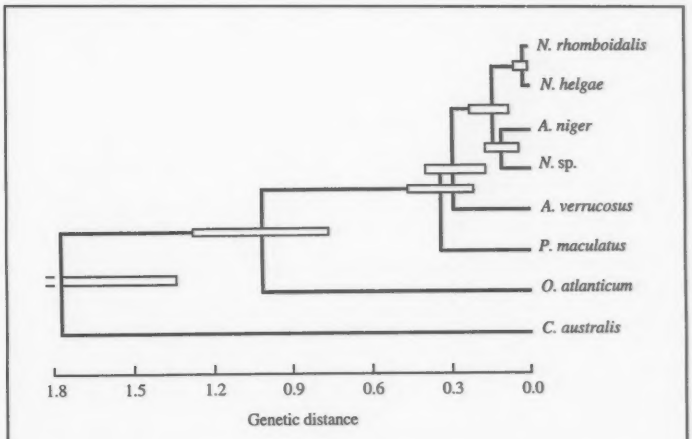

Figure 2

Unweighted pair-group method with arithmetic averaging (UPGMA) phenogram constructed from Nei's (1978) unbiased genetic distance. Open boxes represent standard errors (Nei, 1987) of the branch nodes.

Table 6

Allozyme differences between pairs of oreo species. Above the diagonal: diagnostic loci (no shared alleles); below the diagonal: loci at which significant differences (χ^2 test, $P<0.05$ with Bonferroni adjustment) exist in allele frequencies at loci where alleles are shared, including the GPI-*A** locus. Note that the general protein (PROT) staining patterns (not included here but see Fig. 1) are diagnostic for all species. Total numbers are shown in bold and each locus is identified by the reference number shown in Tables 2 and 3. Species abbreviations are defined in Table 1.

	AN	AV	NA	NH	NR	OA	PM
AN		**3** 1,18,22	**1** 23	**1** 7	**1** 7	**13** 1,2,4, 7,9 12,13,14,15 16,18,19,23	**3** 4,12,21
AV	**10** 6,8,11,12 17,20,23 24,25,26		**3** 18,22,23	**3** 7,18,22	**3** 7,18,22	**14** 1,2,4,7,9,12 13,14,15,16 18,19,22,23	**7** 1,4,6,12 18,21,22
NA	**9** 2,6,7,11 16,17,20 25,26	**8** 1,2,6,7 16,20,24 26		**1** 23	**0**	**12** 1,2,4,9,12,13 14,15,16,18, 19,23,24	**5** 4,6,12,21 23
NH	**9** 3,11,12 17,20,23 24,25,26	**9** 1,6,8,11 12,20,24 26,*GPI-A**	**7** 6,7,12,16 20,24,26		**0**	**13** 1,2,4,9,12,13, 14,15,16,18, 19,23,24	**5** 4,6,7,12 21
NR	**11** 1,3,6,11 12,17,20 23,24,25 26	**11** 1,3,6,8 11,12,20 23,25,26 *GPI-A**	**8** 2,6,7,11, 16,20,23 24	**5** 8,11,12,26 *GPI-A**		**11** 1,2,4,9,12,13, 14,16,18,19, 23	**4** 4,7,12,21
OA	**6** 8,17,20 24,25,26	**8** 6,8,11,20 24,25,26 *GPI-A**	**6** 6,7,8,11, 24,26	**4** 8,20,26 *GPI-A**	**8** 8,11,15,20 24,25,26 *GPI-A**		**14** 1,2,4,6,7,9 12,13,14,16 18,19,21,23
PM	**12** 3,6,8,15 16,17,20 22,23,24 25,26	**10** 3,8,11,15 16,20,23 24,25,26	**8** 1,2,7,11 15,22,24 26	**9** 1,11,15 16,20,22 24,25,26	**13** 1,3,6,8 11,15,16 20,22,23 24,25,26	**7** 8,15,20,22, 24,25,26	

length, all again showing the divergence of *O. atlanticum* , but this time defining some structure to the other species. The 50% majority-rule consensus tree is shown in Figure 4. The most significant difference in this analysis from the two phenetic analyses is the reversal of the positions of the two *Allocyttus* species. In the cladistic analysis *A. niger* is separated from the other species, whereas *A. verrucosus* was grouped with either *P. maculatus* and *N.* sp. or the other two *Neocyttus* species. Applying a topological constraint to the search (enforcing predetermined groupings and keeping only those trees that satisfy the constraints) for the three *Neocyttus* species or the two *Allocyttus* species produced the shortest trees only one step longer than the most parsimonious under no-constraint searches. A search for near-optimal trees with lengths of 53 units produced 56 trees, with 98% confirming the branch separation of *O. atlanticum*, and 71% supporting the separation of *N. rhomboidalis* and *N. helgae* from the other four species, among which the branching points could not be resolved.

The zeids appear to be the most likely sister family to the oreosomatids after the cladistic analyses.

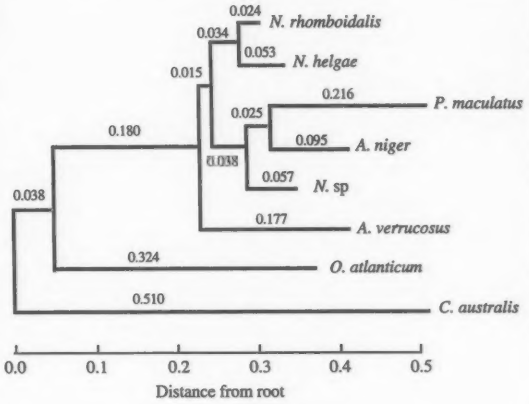

Figure 3

Tree constructed from Rogers' distance by the distance-Wagner procedure. Numbers represent relative branch lengths.

Neither analysis with the berycid or the acanthurid produced the shortest trees that resembled in any way the trees produced from the phenetic analyses or the cladistic analyses with either all three outgroups or *C. australis* alone. *Naso tuberosus* as the outgroup resulted in a single shortest tree (49 units) with *A. verrucosus* as the most divergent oreosomatid and *O. atlanticum* grouped next to the *N. rhomboidalis* and *N. helgae* cluster. Four shortest trees (42 units) resulted from the analysis with *B. splendens*, all of which, although confirming the divergence of *O. atlanticum*, resulted in *N. rhomboidalis* and *N. helgae* diverging independently from the other four species.

Discussion

The mean heterozygosity per locus for the seven oreosomatid species ranged from 8.3% to 18.1%, with an overall mean of 11.8%. These figures are considerably higher than the mean of 5.1% for 195 species of marine and freshwater fish (Ward et al., 1992) and 5.5% for 106 species of marine teleosts (Smith and Fujio, 1982). Three of the seven oreosomatid species had mean heterozygosity values (12.1% to 18.1%) which exceeded the highest value of 11.7% reported by Ward et al. (1994) from comparisons of genetic diversity among populations of 57 species of marine fish. This value was shown by two species, *Fundulus heteroclitus* (Linnaeus, 1766) (15 loci, Ropson et al., 1990) and *Hoplostethus atlanticus* (22 loci, Smith, 1986). Subsequent studies of additional loci in the orange roughy, *H. atlanticus*, raised the estimate of its mean heterozygosity to 13.0% (Elliott and Ward, 1992).

Two or more samples contributed to these heterozygosity estimates for five of the oreo species (Table 1). These estimates of heterozygosity are Hardy-Weinberg expected heterozygosities based on pooled allele frequencies. Had there been substantial differentiation of allele frequencies among samples, such estimates of heterozygosity would have been higher than average sample heterozygosities. In fact, the degree of inter-sample differentiation was, with a single exception, very limited (Lowry et al., unpubl. data). Thus these estimates of total heterozygosity will be very similar to estimates of sample heterozygosity. The one exception was the locus *sSOD** in *N. rhomboidalis*. Variation at this locus was found to be depth-related; samples with a high frequency (>0.6 [cf. <0.2]) of *sSOD**140 came from deeper water (>700 m). The total heterozygosity for this one locus was 0.500, whereas its average sample heterozygosity was 0.285. Use of sample heterozygosity rather than total heterozygosity would effect a small reduction in the overall heterozygosity estimate for this species (from 0.127 to 0.119). Note also that the species with the highest degree of variation, *N.* sp., came from a single sample. The high variability seen in the oreos cannot be attributed to inter-sample differentiation.

It is clear that oreosomatids have higher heterozygosities than most species of teleosts. Interestingly, both oreosomatids and the similarly variable orange roughy occupy deepwater habitats. As speculated by

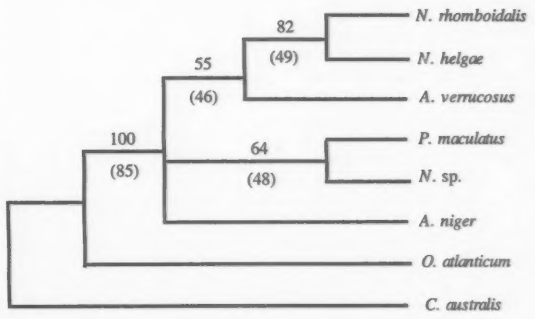

Figure 4

The 50% majority-rule consensus tree of the eleven shortest trees produced by PAUP analysis, with numbers representing the percentage consensus measures for the eleven trees. Numbers in brackets are bootstrapped values (100 replicates).

Elliott and Ward (1992) for the orange roughy, the high heterozygosity shown by these deepwater (500–1200 m) species may reflect their large (prior to exploitation) population sizes and (assuming that deepwater species have been less severely affected by glaciations than shallow water species) a lack of severe bottlenecks in their recent evolutionary past.

As adults, *Pseudocyttus* is the most morphologically distinct oreosomatid genus (James et al., 1988). Its distinguishing characters include the first dorsal-fin spine being longer than the second (vice versa in other species), a pelvic fin with only five rays (usually six or seven in other species), and 40–43 vertebrae (34–41 in other species). However, as juveniles, the genus *Oreosoma* is the most distinctive with prominent cones over the body. Other juvenile oreosomatids have "warts" or protuberances (such structures are absent in at least *N. rhomboidalis)*, but none are quite so pronounced or bizarre as in *O. atlanticum*. Our genetic study confirms the uniqueness of *O. atlanticum*, which has a very low genetic identity (0.371) with the other oreosomatid species—substantially less than the corresponding mean identity (0.650) of *P. maculatus* with other oreosomatids. Morphologically, *O. atlanticum* can be distinguished as an adult by a very large eye (eye diameter 52–60% of head length) and by a prominent horizontal ridge on the operculum.

James et al. (1988) suggested that further study may synonymize the Northern Hemisphere *N. helgae* with the Southern Hemisphere *N. rhomboidalis*. Our allozyme data suggest that, although these two taxa are indeed very closely related (genetic identity I=0.973 for 26 loci and I=0.966 for 27 loci including *GPI-1**), their distinctive muscle protein patterns, not included in the genetic identity values, are consistent with their being separate species. Of the four non-*CK-A** protein bands, two appear to be fixed differently for the two species. However, the amount of genetic differentiation between these two species is only a little greater than that between samples of *H. atlanticus* taken from the same two areas (North Atlantic and off southern Australia) (Elliott et al., 1994). Eleven polymorphic loci were screened in the *H. atlanticus* comparison and just three loci showed significant heterogeneity and gave a genetic identity of 0.990 (N.G.E.'s unpubl. data). Thus the genetic data do not unequivocally validate the recognition of *N. rhomboidalis* and *N. helgae* as distinct species. Morphologically they are also very similar, although there are some differences (Yearsley and Last[2]).

As mentioned earlier, there is depth-related variation in the *sSOD** polymorphism in *N. rhomboidalis*, with samples derived from deeper water having a high frequency of *sSOD**140. We are uncertain as yet whether this indicates reproductive isolation of two forms or selection acting on *sSOD*, although the lack of detectable mitochondrial DNA differentiation (Grewe, Innes, and Evans[4]) suggests that if reproductive isolation is responsible, it is likely to be recent in origin. These data and analyses will be presented in full elsewhere.

The new species *N.* sp., infrequently captured with *P. maculatus* and *A. niger* in southern Australian waters and morphologically similar to *N. rhomboidalis*, showed quite a high degree of genetic similarity to the other two *Neocyttus* species (I=0.903 with *N. rhomboidalis* and 0.884 with *N. helgae*). However, it was genetically distinct from them at several loci (Table 6), and numerous meristic and morphological characters (Yearsley and Last[2]) confirm that it is a separate species. Although it clustered with *A. niger* (I=0.903) in the two phenetic trees constructed from the genetic distance data, in the cladistic analyses it grouped more often with *P. maculatus*. However, classical taxonomic techniques suggest a close association with *Neocyttus* species, particularly the western Indian Ocean *N. acanthorhynchus* (Yearsley and Last[2]).

The two *Allocyttus* species were found to be genetically quite distinct from one another (I=0.695); there was no evidence from either phenetic or cladistic analyses that they made up an exclusive monophyletic group. James et al. (1988) gave no justification for placing *A. niger* in *Allocyttus*. However, they drew attention to problems with generic diagnoses of the oreosomatids. *Allocyttus*, as it currently stands, but excluding *A. niger* (i.e. *A. verrucosus*, *A. guineensis*, and *A. folletti*), may be a natural grouping, with *A. niger* more akin to, but probably not congeneric with, *Neocyttus*. Ongoing morphological work should elucidate these problems.

Whereas the branch node for *O. atlanticum* is clearly resolved to be ancestral to the remaining oreosomatids, the phenetic and cladistic analyses could not resolve unambiguously all the internal nodes for the remaining species. There is strong evidence for a branch node separating *N. rhomboidalis* and *N. helgae* from the other four species, but there is no evidence supporting two species in *Allocyttus*.

Several problems in the family Oreosomatidae remain to be resolved. They include the formal description of the rough oreo, *N.* sp. (Yearsley and Last[2]), a reassessment of the generic affinities of *A. niger* and *A. verrucosus*, and further examination of the two depth-related *sSOD** forms of *N. rhomboidalis* and their relationship to *N. helgae*. As intimated by

[4] Grewe, P. M., B. H. Innes, and B. S. Evans. 1995. CSIRO Division of Fisheries, Castray Esplanade, Hobart, Tasmania 7000, Australia.

James et al. (1988), there remains a clear need for a full and thorough revision of the family Oreosomatidae.

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Is fish recruitment related to spawner abundance?

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Abstract.—We analyzed 364 spawner-recruitment time series to determine whether recruitment is related to spawner abundance. We pose three questions: 1) Does the highest recruitment occur when spawner abundance is high? 2) Does the lowest recruitment occur when spawner abundance is low? and 3) Is the mean recruitment higher if spawner abundance is above rather than below the median? We found that when there is a sufficient range in spawner abundance the answer to all three questions is almost always "yes." Thus, spawner abundance cannot be ignored in the management of fish populations. Recruitment overfishing appears to be a common problem.

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Perhaps the most fundamental issue for the study and management of fish populations is the relation between spawner abundance and subsequent recruitment. There is surprisingly little consensus on this issue; many researchers believe that there is no relevant relationship between species abundance and recruitment (reviewed by Wooster and Bailey, 1989; Koslow et al., 1987) whereas others believe it to be fundamental (e.g. Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971; Myers et al., 1995a). The assumed absence of a relationship between spawner abundance and recruitment has prompted some scientists to claim that recruitment overfishing is almost impossible (Laevastu, 1993). This divergence of opinion has practical consequences for the management of fisheries: many fisheries are managed without consideration of maintaining a sustainable abundance or biomass of spawners (Smith et al., 1993).

The purpose of this paper is to provide conclusive evidence that strong year classes are more likely when spawner abundance is large. We approach the problem using the simplest possible nonparametric methods in order to avoid the many subtle statistical difficulties in fitting spawner-recruitment functions (Walters, 1985, 1990; Hilborn and Walters, 1992). Our approach is to examine systematically 364 data sets from the most recent version of the database compiled by Myers et al. (1995b) as part of an ongoing study of recruitment variability. By analyzing many populations with identical methods, it is possible to arrive at conclusions with greater reliability.

The nonparametric methods we used were devised in order to answer three deliberately simple questions. First: Does the largest recruitment occur when the spawner abundance is high? To answer this question, we examined the rank of spawner abundance associated with the largest recruitment. Second: Does the smallest recruitment occur when spawner abundance is low? This time we examined the rank of spawner abundance associated with the smallest recruitment. Third: Is the mean recruitment higher if spawner abundance is above rather than below the median? To answer this question, we examined the ratio of mean recruitment when spawner abundance is above the median to mean recruitment when spawner abundance is below the median.

Data

By "spawner abundance" we mean any of the following metrics of the size of the spawning stock: spawning stock biomass, the number of spawners, the number of eggs, or some index of spawner abundance (derived from catch per unit of effort or research vessels).

We tried to assemble all time series of reliable data on spawner abundance and recruitment. We started with the 477 time series from the most recent version of the database by Myers et al. (1995b). Of these, 77 series were eliminated because they had less than 5 years of spawner-recruitment data, 5 series were eliminated because they were for invertebrates, 17 pink and chum salmon series were eliminated because they were described as less reliable, and 14 series were eliminated because they were different versions of other series or because they overlapped other series. We were left with 364 series. Sometimes the same population was included more than once because of incompatible time periods or because different life stages were examined.

For each population, Table 1 lists the method used to estimate spawner abundance and recruitment. For most marine populations, spawning biomass and recruitment had been estimated by sequential population analysis (SPA) of commercial catch-at-age data. SPA techniques include virtual population analysis (VPA; Gulland[1]), cohort analysis (Pope, 1972), and related methods that reconstruct population size from catch-at-age data (Deriso et al., 1985, 1989; Megrey, 1989; Gavaris, 1988). For some marine populations, accurate commercial catch-at-age data were not available; therefore research vessel (RV) surveys estimates were used. For a few populations, other types of data were used, e.g. spawning stock biomass was estimated from SPA and recruitment was estimated from research vessel surveys. We did not include populations for which there was only commercial catch-per-unit-of-effort estimates of abundance.

For populations in the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted in Table 1 as follows: a = adults (or eggs); f = fry; s = smolts (sea-bound migrating juveniles); and p = parr (juveniles within the river).

For most of the Pacific salmonid populations, the numbers of spawners and recruits were reconstructed from commercial catch-at-age data and independent estimates of fishing mortality or from an independent estimate of escapement from surveys of spawning, or both. In these cases, the method is termed "stock reconstruction," and is denoted as SR in Table 1. Some of the estimates were derived from experiments in which the number of spawners and recruits, e.g. number of parr produced, are direct counts. We analyzed data by families and species separately if there were at least 6 populations per taxa.

[1] Gulland, J. A. 1965. Estimation of mortality rates. Annex to Rep., Arctic Fish. Working Group ICES Council Meeting 1965(3), 9 p.

Methods and results

In evaluating the relationship between spawners and recruitment, the range of the spawner data will clearly be important. For near constant spawner levels, changes in recruitment will reflect only variability in density-independent mortality. As an index of the range spanned by the spawner data, we used the ratio S_{max}/S_{min}, where S_{max} is the maximum observed spawner abundance and S_{min} is the minimum observed spawner abundance. When this ratio is near 1, the spawner level is nearly constant; the larger its value, the greater the range of spawner data. Values of S_{max}/S_{min} for the data series examined in this paper are listed in Table 1.

Hypothesis 1: Does the largest recruitment occur when spawner abundance is high?

For each spawner-recruitment series we asked whether the highest recruitment, R_{max}, occurred when spawner abundance was high. We computed the rank of the spawner abundance that gave rise to the highest recruitment, S_{Rmax}. In order to compare ranks across populations, we computed a "relative rank" $r_{max} = (\text{rank}(S_{Rmax}) - 1)/(n - 1)$, where n is the number of observations in the spawner-recruitment series (Fig. 1A). The relative rank therefore lies between 0 and 1, with $r_{max} = 0$ implying that the highest recruitment occurs for the lowest spawner abundance, and conversely, with $r_{max} = 1$ implying that the highest recruitment occurs for the highest spawner abundance.

To help summarize the data and to test hypotheses, cumulative weighted means were calculated. The weighted mean of k relative ranks $r_{max,i}$ is

$$\frac{\sum_{i=1}^{k} n_i r_{\max,i}}{\sum_{i=1}^{k} n_i}, \qquad (1)$$

where n_i is the number of observations in the ith spawner-recruitment series. The cumulative weighted mean was calculated by starting with the relative rank associated with the largest value of S_{max}/S_{min} and by continuing through the relative rank associated with the smallest value of S_{max}/S_{min}.

If, for a given population, spawner abundance and highest recruitment were independent, each possible relative rank would be equally likely, i.e. the expected value of $r_{max,i}$ would be 0.5. If this were true for each population, then the expected value of the weighted mean relative rank would also be 0.5. Therefore we

Table 1

Statistics for each population. "Population" lists the order, family, species, and location; n lists the number of common years of spawner-recruitment data; S_{max}/S_{min} lists the ratio of maximum quantity of spawners to minimum quantity of spawners; r_{max} lists the relative rank of the quantity of spawners for the maximum recruitment; r_{min} lists the relative rank of the quantity of spawners for the minimum recruitment; $\overline{R}_{above}/\overline{R}_{below}$ lists the ratio of mean recruitment above the median quantity of spawners to mean recruitment below the median quantity of spawners; and "Method" lists the stock assessment method used (SPA=sequential population analysis, Count=direct count, RV=research vessel, SR=stock reconstruction, MR=mark recapture). For populations within the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted as follows: a = adults (or eggs), f = fry, s = smolt, and p = parr. They are shown in the table with an arrow notation so that "a ⇒ f" means spawners were "adults" and recruits were "fry."

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Aulopiformes						
Synodontidae						
Greater lizardfish (*Saurida tumbil*)						
East China Sea	10	6.8	0.67	0.22	1.7	CPUE
Clupeiformes						
Clupeidae						
Blueback herring (*Alosa aestivalis*)						
Saint John River	14	65.2	0.77	0.08	2.9	Count
Alewife (*Alosa pseudoharengus*)						
Damariscotta Lake, Maine	8	5.6	0.21	0.43	1.0	Count
Lake Ontario	7	7.4	0.50	0.00	0.3	RV
Saint John River	16	54.8	1.00	0.33	2.2	Count
Anadromous American shad (*Alosa sapidissima*)						
Connecticut River	16	4.5	0.67	0.20	1.2	MR and count
Gulf menhaden (*Brevoortia patronus*)						
Gulf of Mexico	19	11.2	0.78	0.17	1.2	SPA
Atlantic menhaden (*Brevoortia tyrannus*)						
U.S. Atlantic	35	39.8	0.79	0.32	1.5	SPA
Herring (*Clupea harengus*)						
Archipelago and Bothnian Seas	13	1.3	0.33	1.00	0.7	SPA
Baltic, Bothnian Sea	15	1.6	0.93	0.79	0.9	SPA
S.W. Baltic	19	2.8	0.39	0.94	0.8	SPA
S. Baltic	15	1.2	0.57	0.07	1.0	SPA
Central Baltic	16	1.4	0.67	0.53	1.4	SPA
Baltic, Bothnian Bay	15	1.7	0.93	0.29	1.8	SPA
Central Coast B.C.	38	16.4	0.78	0.16	1.0	SPA
Craig, Alaska	16	13.4	0.53	0.73	2.6	SPA
Downs stock	65	470.5	0.84	0.02	5.5	SPA
Eastern Bering Sea	26	16.7	0.20	0.68	0.6	SPA
Georges Bank	15	9.9	0.50	0.14	1.2	SPA
Gulf of Finland	18	1.8	0.94	1.00	0.9	SPA
Gulf of Maine	23	6.6	0.09	0.95	0.8	SPA
Gulf of Riga	19	2.2	0.11	0.44	1.3	SPA
West of Scotland	18	10.4	0.76	0.53	1.2	SPA
West of Ireland	19	2.5	0.78	1.00	0.8	SPA
Iceland (spring spawners)	23	630.0	0.45	0.00	1.4	SPA
Iceland (summer spawners)	46	39.6	0.91	0.04	2.9	SPA
N. Gulf of St. Lawrence (fall spawners)	13	4.7	0.33	0.67	0.2	SPA
N. Gulf of St. Lawrence (spring spawners)	13	6.0	0.33	0.75	0.3	SPA
S. Gulf of St. Lawrence (fall spawners)	9	9.1	0.62	0.38	1.2	SPA
S. Nova Scotia	11	6.2	0.90	0.40	1.4	SPA
North Sea	41	76.1	0.68	0.15	1.7	SPA
North Strait of Georgia	38	22.4	0.65	0.27	1.4	SPA
North West Coast Vancouver Island	38	13.0	0.95	0.54	1.0	SPA
Northern Irish Sea	18	5.5	0.94	0.12	1.3	SPA
Norway (spring spawners)	41	8,986.4	1.00	0.03	5.5	SPA

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Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Prince Rupert District	38	11.3	0.97	0.35	1.2	SPA
Queen Charlotte Islands	38	34.2	0.73	0.14	1.2	SPA
Revilla Channel (Kah Shakes), Alaska	16	3.1	0.33	0.47	0.6	SPA
S.E. Alaska	30	6.0	0.03	0.52	1.2	SPA
Seymour Canal, Alaska	16	8.4	0.73	0.33	1.0	SPA
Sitka, Alaska	21	14.8	0.95	0.15	3.2	SPA
South West Coast Vancouver Island	38	42.0	0.86	0.22	1.0	SPA
Southern Central Baltic	11	1.9	0.80	0.00	1.4	SPA
Southern Strait of Georgia	38	8.4	0.49	0.05	0.9	SPA
Yellow Sea or Huanghai Sea	15	51.2	0.93	0.79	1.9	SPA
Spanish sardine (*Sardina pilchardus*)						
Iberian Atlantic Coast	14	5.7	0.96	0.46	0.9	SPA
Brazilian sardine (*Sardinella brasiliensis*)						
South Eastern Brazil	15	3.4	0.57	0.00	1.6	Length-based SPA
Sardine (*Sardinops sagax*)						
California	31	134.4	0.87	0.00	6.4	SPA
Chile-Northern zone	13	4.1	1.00	0.25	1.0	SPA
Gulf of California	13	15.1	0.75	0.17	2.2	SPA
Eastern Japan	14	6.4	0.15	0.77	0.6	SPA
Sea of Japan	13	26.2	0.58	0.92	1.7	SPA
South Africa	31	19.0	0.53	0.83	1.7	SPA
South Africa	8	69.2	0.00	1.00	0.8	SPA
Sprat (*Sprattus sprattus*)						
Central Baltic	15	5.6	0.93	0.43	0.7	SPA
S.E. Baltic	19	19.7	0.11	0.50	1.7	SPA
Engraulidae						
S.A. anchovy (*Engraulis capensis*)						
South Africa	18	3.5	0.00	0.53	1.3	SPA
South Africa	10	3.7	0.67	0.06	2.5	Acoustics
Northern anchovy (*Engraulis mordax*)						
California	25	4.7	0.79	0.33	0.9	SPA
Peruvian anchoveta (*Engraulis ringens*)						
Northern and central stock, Peru	19	18.4	0.61	0.00	2.2	SPA
Cypriniformes						
Cyprinidae						
Bream (*Abramis brama*)						
Lake Tjeukemeer, the Netherlands	11	4.5	0.50	0.30	0.5	RV
Golden shiner (*Notemigonus crysoleucas*)						
Lake St. George, Ontario	8	6.7	0.43	0.29	0.2	MR and beach seine
Roach (*Rutilus rutilus*)						
Klicava Reservoir	11	1.9	0.00	0.40	0.8	MR
Gadiformes						
Gadidae						
Pacific cod (*Gadus macrocephalus*)						
Eastern Bering Sea	10	5.8	0.33	0.22	0.8	SPA
Hecate Strait	14	2.9	0.62	0.15	1.5	SPA
Cod (*Gadus morhua*)						
S.E. Baltic	22	5.3	0.43	0.10	1.4	SPA
Central Baltic	22	5.4	0.52	0.24	1.7	SPA
Celtic Sea	20	4.4	0.89	0.53	1.6	SPA
Faroe Plateau	31	6.7	0.58	0.20	0.9	SPA
Eastern English Channel	12	4.3	0.73	0.18	1.4	SPA
West of Scotland	27	3.7	0.10	1.00	0.8	SPA

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Iceland	38	7.3	0.49	0.08	1.2	SPA
Irish Sea	25	3.6	0.17	1.00	0.8	SPA
Kattegat	21	12.7	1.00	0.10	1.8	SPA
W. Coast of Greenland	31	55.7	0.83	0.30	2.3	SPA
Labrador and N.E. Newfoundland	28	17.2	0.93	0.28	2.7	SPA
Flemish Cap	10	18.7	0.56	0.78	2.6	RV
S. Grand Banks	31	9.0	0.67	0.53	1.9	SPA
N. Gulf of St. Lawrence	17	4.7	0.31	0.06	1.0	SPA
St. Pierre Bank	31	4.2	0.83	0.00	1.2	SPA
S. Gulf of St. Lawrence	41	5.9	0.66	0.19	1.1	SPA
E. Scotian Shelf	33	4.7	0.75	0.25	1.1	SPA
S.W. Scotian Shelf	45	2.0	0.64	0.66	1.0	SPA
Gulf of Maine	7	1.8	0.17	0.50	0.6	SPA
Georges Bank	14	1.7	0.00	0.15	1.2	SPA
North East Arctic	43	15.8	0.81	0.02	1.6	SPA
North Sea	28	4.4	1.00	0.22	1.2	SPA
Skagerrak	13	2.3	0.50	0.42	1.1	SPA
Haddock (*Melanogrammus aeglefinus*)						
Faroe Plateau	30	4.1	0.72	0.00	1.1	SPA
West of Scotland	28	10.9	0.41	0.33	0.7	SPA
Iceland	28	8.6	0.48	0.52	0.8	SPA
E. Scotian Shelf	38	23.2	0.84	0.32	2.9	SPA
S.W. Scotian Shelf	24	3.7	0.91	0.00	1.2	SPA
Georges Bank	58	17.2	0.93	0.02	2.7	SPA
North East Arctic	41	12.0	0.93	0.12	2.0	SPA
North Sea	31	23.4	0.52	0.17	0.8	SPA
Rockall Bank	6	4.1	0.20	0.80	0.5	SPA
Whiting (*Merlangius merlangus*)						
Celtic Sea	9	2.9	0.75	0.88	1.1	SPA
Eastern English Channel	14	3.9	0.46	0.38	1.2	SPA
West of Scotland	27	4.1	0.56	0.23	1.2	SPA
Irish Sea	13	3.2	0.58	1.00	1.0	SPA
North Sea	27	2.7	0.38	0.62	0.9	SPA
Silver hake (*Merluccius bilinearis*)						
Mid Atlantic Bight	33	27.1	0.88	0.31	2.9	SPA
Scotian Shelf	13	2.0	0.67	0.75	1.2	SPA
Georges Bank	33	25.3	0.78	0.28	5.1	SPA
S.A. hake (*Merluccius capensis*)						
South Africa	20	5.6	0.74	0.58	1.1	SPA
South Africa South Coast	12	1.5	0.64	1.00	1.0	SPA
Peruvian hake (*Merluccius gayi*)						
Chile-South Central zone	14	1.7	0.15	1.00	0.8	SPA
Chile-Northern zone	14	2.4	0.85	0.54	1.3	SPA
Peru	8	3.0	0.43	1.00	0.6	SPA
Hake (*Merluccius merluccius*)						
West of France and British Isles	14	1.8	1.00	0.31	1.0	SPA
Iberian Atlantic Coast	9	3.2	0.88	0.00	2.0	SPA
Jabuka Pit, Adriatic Sea	26	8.5	1.00	0.20	1.1	CPUE
Pacific hake (*Merluccius productus*)						
W. U.S. + Canada	33	2.2	0.06	1.00	1.0	SPA
Blue whiting (*Micromesistius poutassou*)						
N.E. Atlantic (North)	20	3.5	0.21	0.79	0.6	SPA
N.E. Atlantic (South)	10	1.2	1.00	0.72	1.1	SPA
Pollock or saithe (*Pollachius virens*)						
Faroe	30	2.4	0.03	0.93	0.8	SPA

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Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
West of Scotland	20	3.2	0.39	0.79	0.8	SPA
Iceland	26	4.1	0.56	0.26	1.0	SPA
Scotian Shelf and Georges Bank	10	1.7	0.78	0.33	1.5	SPA
North East Arctic	32	8.9	0.19	0.06	1.3	SPA
North Sea	22	7.0	0.95	0.10	1.1	SPA
Walleye pollock (*Theragra chalcogramma*)						
E. Bering Sea	24	5.9	0.26	0.83	0.8	SPA
East Kamchatka	12	24.0	1.00	0.27	2.0	SPA
Gulf of Alaska, Alaska	25	4.3	0.38	0.50	0.5	SPA
Japan-Pacific Coast of Hokkaido	15	3.8	0.29	0.43	0.9	SPA
West Bering Sea	8	2.8	1.00	0.00	2.1	SPA
Norway pout (*Trisopterus esmarkii*)						
North Sea	12	4.3	0.45	0.27	1.2	SPA
Red hake (*Urophycis chuss*)						
Gulf of Maine and N. Georges Bank	13	8.6	0.50	0.17	1.4	SPA
S. New England	15	5.7	0.64	0.07	2.6	SPA
White hake (*Urophycis tenuis*)						
S. Gulf of St. Lawrence	14	2.7	0.08	0.38	0.7	SPA
Lophiformes						
Lophiidae						
Monkfish (*Lophius piscatorius*)						
Celtic Sea and West of France	6	1.6	1.00	0.40	2.7	SPA
Perciformes						
Ammodytidae						
Sandeel (*Ammodytes marinus*)						
West of Scotland	10	8.5	0.44	0.78	0.8	SPA
Northern North Sea	14	7.1	0.08	0.23	0.7	SPA
Shetland	16	4.4	0.93	0.47	1.3	SPA
Southern North Sea	14	6.1	0.77	1.00	1.6	SPA
Branchiostegidae						
Branquillo (*Branchiostegus japonicus*)						
Wakasa Bay	7	2.4	0.50	0.92	0.4	Leslie
Carangidae						
Cape horse mackerel (*Trachurus capensis*)						
Namibian Coast	17	3.9	0.31	0.94	0.5	SPA
Horse mackerel (*Trachurus symetricus murphyi*)						
South Pacific Ocean	15	5.5	0.50	0.79	1.1	SPA
Horse mackerel (*Trachurus trachurus*)						
Iberian Atlantic Coast	8	1.7	0.14	0.43	0.6	SPA
N.E. Atlantic	8	4.3	0.14	0.00	0.2	SPA
Lactariidae						
False trevally (*Lactarius lactarius*)						
Gulf of Thailand	8	521.8	0.43	0.00	0.9	CPUE
Lutjanidae						
Silk snapper (*Lutjanus synagris*)						
Cuba	17	2.8	0.44	0.38	1.0	SPA
Mugilidae						
Grey mullet (*Mugil cephalus*)						
Taiwan	7	2.3	1.00	0.17	1.3	SPA
Pentacerotidae						
Pelagic armourhead (*Pseudopentaceros wheeleri*)						
Southeast Hancock Seamount, Hawaii	11	19.1	1.00	0.70	7.1	Leslie
Percidae						
Yellow perch (*Perca flavescens*)						

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Oneida Lake, New York	7	1.6	0.00	0.67	0.3	Seine
South Bay, Lake Huron	27	582.9	0.62	0.58	1.6	Research nets
Eurasian perch (*Perca fluviatilis*)						
Lake Ijssel, the Netherlands	16	6.2	0.50	0.77	0.8	SPA, RV
Pikeperch (*Stizostedion lucioperca*)						
Lake Ijssel, the Netherlands	17	43.0	0.50	1.00	0.5	SPA, RV
Walleye (*Stizostedion vitreum*)						
Escanaba Lake, Wisconsin	16	3.9	0.07	0.60	0.4	MR
Lake Erie	14	23.7	0.23	0.77	0.6	SPA
Lake Erie, Michigan	22	452.7	0.81	0.14	3.6	CPUE
Mille Lacs Lake, Minnesota	12	3.3	0.91	0.45	5.2	SPA
Rainy Lake, Minnesota	15	2.1	0.93	0.00	1.6	CPUE
Scianidae						
White croaker (*Argyrosomus argentatus*)						
East China Sea	15	1.9	0.79	0.64	1.1	SPA
Black croaker (*Argyrosomus nibe*)						
East China Sea	13	61.0	0.58	0.17	2.3	CPUE
Yellow croaker (*Pseudociaena polyactis*)						
East China Sea	10	15.0	0.78	0.22	2.7	Catch curve
Scombridae						
Chub mackerel (*Scomber japonicus*)						
Pacific Coast of Japan	16	33.5	0.27	0.53	0.4	Egg survey
Pacific Coast of Japan	12	33.5	1.00	0.09	2.6	Egg survey
Southern California	36	64.1	0.89	0.23	2.5	SPA
Mackerel (*Scomber scombrus*)						
N.W. Atlantic	28	10.7	0.30	0.44	1.1	SPA
N.E. Atlantic	19	1.9	0.56	0.50	1.0	SPA
Yellowfin tuna (*Thunnus albacares*)						
Eastern Pacific Ocean	25	3.4	0.88	0.58	1.4	SPA
Indian Ocean	25	9.1	0.83	0.04	2.2	SPA
Southern bluefin tuna (*Thunnus maccoyii*)						
Southern Pacific	26	4.2	0.64	0.04	1.2	SPA
Atlantic bluefin tuna (*Thunnus thynnus*)						
West Atlantic	23	8.2	0.91	0.00	2.2	SPA
Sparidae						
Sea bream (*Chrysophrys major*)						
Yellow Sea	17	440.3	0.81	0.00	2.2	CPUE
Red porgy (*Pagrus pagrus*)						
Atlantic Ocean off North Carolina	14	3.0	0.23	0.00	1.2	SPA
Yellow sea bream (*Taius tumifrons*)						
Central East China Sea	20	4.3	0.26	0.00	1.7	Catch curve
East China Sea	8	3.2	0.00	0.57	0.7	CPUE
Japan Coast	20	6.2	0.89	0.05	2.1	Catch curve
South East China Sea	18	9.9	1.00	0.00	3.8	Catch curve
Pleuronectiformes						
Bothidae						
Summer flounder (*Paralichthys dentatus*)						
Middle Atlantic Bight	9	3.1	1.00	0.12	1.8	SPA
Pleuronectidae						
American plaice (*Hippoglossoides platessoides*)						
Grand Banks	19	4.0	0.72	0.28	1.3	SPA
Georges Bank	11	6.3	0.00	0.70	0.6	SPA
Pacific halibut (*Hippoglossus stenolepis*)						
Pacific	47	2.8	0.39	0.46	0.9	SPA
Rock sole (*Lepidopsetta bilineata*)						

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Hecate Strait, B.C.	24	4.6	0.39	0.70	1.0	CPUE
Yellowfin sole (*Limanda aspera*)						
E. Bering Sea	12	1.9	0.91	0.45	1.3	SPA
Yellowtail flounder (*Limanda ferruginae*)						
Grand Banks	15	3.1	0.50	0.00	1.0	SPA
Georges Bank	20	11.8	0.95	0.21	2.7	SPA
Southern New England	20	16.7	0.63	0.00	1.1	SPA
Plaice (*Pleuronectes platessa*)						
Celtic Sea	14	3.4	0.85	0.31	1.2	SPA
Skagerrak and Kattegat	12	2.2	0.45	0.73	0.5	SPA
Eastern English Channel	11	2.2	0.60	0.10	1.3	SPA
Western English Channel	15	2.9	0.71	0.00	1.4	SPA
Irish Sea	28	3.7	0.00	0.56	0.9	SPA
Kattegat	22	10.7	0.67	0.14	2.4	SPA
North Sea	35	1.9	0.35	0.63	0.8	SPA
Skagerrak	10	2.2	0.56	0.44	0.9	SPA
Greenland halibut (*Reinhardtius hippoglossoides*)						
W. Greenland and Iceland	14	2.5	0.31	0.92	0.9	SPA
North East Arctic	21	4.3	0.40	0.10	1.3	SPA
Northwest Atlantic	15	2.6	0.14	0.86	0.8	SPA
Scophthalmidae						
Megrim (*Lepidorhombus whiffiagonis*)						
West of France and British Isles	7	1.5	0.83	0.50	1.1	SPA
Iberian Atlantic Coast	6	1.6	0.20	1.00	0.2	SPA
Soleidae						
Sole (*Solea vulgaris*)						
Bay of Biscay (VIII)	13	2.0	0.17	0.75	0.9	SPA
Celtic Sea	18	2.4	0.00	0.88	0.4	SPA
Skagerrak and Kattegat	5	2.2	1.00	0.50	1.4	SPA
Eastern English Channel	20	5.4	0.42	1.00	1.1	SPA
Western English Channel	22	2.7	0.90	0.48	1.3	SPA
Irish Sea	21	2.0	0.00	0.65	0.5	SPA
North Sea	36	5.7	0.96	0.19	1.1	SPA
Salmoniformes						
Esociadae						
Pike (*Esox lucius*)						
North Basin, Windermere Lake	35	7.3	0.74	0.13	1.6	SPA
South Basin, Windermere Lake	35	5.8	0.57	0.07	1.5	SPA
Osmeridae						
Capelin (*Mallotus villosus*)						
Barents Sea	20	138.0	0.79	0.84	2.2	RV
Iceland	12	5.2	0.27	0.36	0.9	SPA
Plecoglossidae						
Ayu (*Plecoglossus altivelis*)						
Lake Biwa, Japan	12	19.3	0.82	0.00	1.0	SPA
Salmonidae						
Lake Whitefish (*Coregonus clupeaformis*)						
Lake Huron (a ⇒ a)	28	77.3	0.78	0.89	1.4	Research nets
Bloater (*Coregonus hoyi*)						
Lake Michigan (a ⇒ a)	11	49.5	0.90	0.10	37.1	RV
Whitefish (*Coregonus lavaretus*)						
Lake Constance, Europe (a ⇒ a)	21	7.9	0.65	0.00	3.2	SPA
Pink salmon (*Oncorhynchus gorbuscha*)						
Auke Creek, Alaska (f ⇒ a)	14	10.4	0.92	0.00	1.6	Count
Auke Creek, Alaska (a ⇒ f)	16	15.5	0.73	0.00	1.6	Count

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Bakhura River, Sakhalin Is. (a ⇒ f)	26	54.0	0.24	0.04	0.7	Count
Bakhura River, Sakhalin Is. (f ⇒ a)	24	35.1	0.65	0.22	1.4	Count
Bakhura River, Sakhalin Is. (a ⇒ a)	24	54.0	0.91	0.13	1.4	Count
Bentinck, B.C. (a ⇒ a)	11	76.4	0.70	0.10	2.4	SR
Brown's Peak Creek, Cook Inlet, Alaska (a ⇒ a)	22	280.0	0.48	0.12	1.1	SR
Bruin Bay, Cook Inlet, Alaska (a ⇒ a)	17	252.4	0.88	0.06	15.1	SR
Central Alaska (a ⇒ a)	25	310.0	0.75	0.17	2.9	SR
Central B.C. (Areas 6–8) (a ⇒ a)	14	4.1	0.77	0.69	1.1	SR
Central Coast Area 7, B.C. (a ⇒ a)	11	4.2	0.80	0.20	1.4	SR
Central Coast Area 9, B.C. (a ⇒ a)	11	51.5	0.70	0.20	4.5	SR
Dagi River, Sakhalin Is. (a ⇒ f)	11	81.0	0.90	0.00	2.3	Count
Desire Lake, Cook Inlet, Alaska (a ⇒ a)	8	12.5	0.14	0.86	0.5	SR
Douglas, B.C. (a ⇒ a)	11	5.2	0.80	0.50	3.4	SR
Fraser River, B.C. (a ⇒ a)	16	6.0	0.93	0.00	1.8	SR
Gardner, B.C. (a ⇒ a)	11	54.0	0.50	0.20	1.5	SR
Hooknose Creek, B.C., Canada (a ⇒ f)	14	35.8	0.85	0.69	4.1	Count
Humpy Creek, Cook Inlet, Alaska (a ⇒ a)	27	37.0	0.85	0.27	1.3	SR
Island Creek, Cook Inlet, Alaska (a ⇒ a)	25	350.0	0.83	0.92	3.9	SR
James Lagoon, Cook Inlet, Alaska (a ⇒ a)	8	12.7	0.43	0.71	0.3	SR
Kitimat, B.C. (a ⇒ a)	11	69.8	0.90	0.10	5.9	SR
Kodiak Archipelago, Alaska (a ⇒ a)	42	37.2	0.76	0.15	2.0	SR
Kodiak Archipelago, Alaska (a ⇒ f)	19	9.6	0.78	0.22	1.5	SR
Lakelse River, B.C. (a ⇒ f)	8	10.8	0.71	0.00	1.9	MR and count
Lakelse River, B.C. (f ⇒ a)	8	4.4	1.00	0.43	2.0	MR and count
Lakelse River, B.C. (a ⇒ a)	9	10.8	0.75	0.88	1.2	MR and count
Lesnaya River, Sakhalin Is. (a ⇒ f)	9	36.1	0.75	0.00	1.4	Count
Lower Skeena, B.C. (a ⇒ a)	11	7.6	0.70	0.30	1.8	SR
Lutoga River, Sakhalin Is. (a ⇒ f)	20	29.7	0.95	0.11	2.4	Count
Lutoga River, Sakhalin Is. (f ⇒ a)	19	17.6	0.94	0.06	2.1	Count
Lutoga River, Sakhalin Is. (a ⇒ a)	19	29.7	1.00	0.33	2.8	Count
North Coast Area 4, B.C. (a ⇒ a)	11	8.9	0.50	0.90	1.1	SR
Northern Panhandle, Alaska (a ⇒ a)	34	6.0	0.92	0.11	2.0	SR
Pokosnaya River, Sakhalin Is. (a ⇒ f)	25	384.6	0.88	0.06	8.1	Count
Pokosnaya River, Sakhalin Is. (f ⇒ a)	24	244.2	0.57	0.04	4.9	Count
Pokosnaya River, Sakhalin Is. (a ⇒ a)	23	384.6	0.82	0.00	6.5	Count
Poronal River, Sakhalin Is. (a ⇒ a)	21	84.1	0.95	0.10	3.1	Count
Port Chatham, Cook Inlet, Alaska (a ⇒ a)	15	69.3	0.86	0.07	4.4	SR
Port Dick, Cook Inlet, Alaska (a ⇒ a)	27	77.3	0.96	0.04	2.3	SR
Port Graham, Cook Inlet, Alaska (a ⇒ a)	27	33.3	0.69	0.58	1.7	SR
Prince William Sound, Alaska (a ⇒ a)	25	17.0	0.58	0.00	2.4	SR
Rocky River, Cook Inlet, Alaska (a ⇒ a)	20	85.0	0.32	0.03	1.4	SR
Sashin Creek, Alaska (a ⇒ f)	25	11,084.8	0.83	0.08	17.1	Count
Seldovia, Cook Inlet, Alaska (a ⇒ a)	27	14.8	0.15	0.23	1.1	SR
Southern Panhandle, Alaska (a ⇒ a)	34	8.3	0.94	0.15	2.3	SR
Sunday Creek, Cook Inlet, Alaska (a ⇒ a)	18	1,090.0	0.71	0.26	2.9	SR
Upper Skeena, B.C. (a ⇒ a)	11	19.6	1.00	0.20	1.5	SR
Utka River, Kamchatka (a ⇒ f)	12	182.0	0.45	0.00	2.0	Count
Utka River, Kamchatka (f ⇒ a)	10	7.7	0.78	0.06	10.4	Count
Utka River, Kamchatka (a ⇒ a)	10	124.7	0.67	1.00	2.9	Count
Windy Left, Cook Inlet, Alaska (a ⇒ a)	27	748.0	0.96	0.08	7.0	SR
Windy Right, Cook Inlet, Alaska (a ⇒ a)	27	187.0	0.88	0.19	3.6	SR
Chum salmon (*Oncorhynchus keta*)						
Central Coast, B.C. (a ⇒ a)	30	4.8	1.00	0.24	1.5	SR
Fraser River, B.C. (a ⇒ a)	14	5.0	1.00	0.00	2.0	SR
Hooknose Creek, B.C. (a ⇒ f)	14	15.4	0.92	0.00	2.5	Count
Johnstone Strait (a ⇒ a)	28	4.7	0.89	0.63	2.0	SR

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Minter Creek, Washington (a ⇒ f)	14	352.5	1.00	0.08	4.2	Count
North Coast, B.C. (a ⇒ a)	30	4.6	0.48	0.24	1.0	SR
Queen Charlotte Islands, B.C. (a ⇒ a)	25	11.0	0.21	0.04	1.0	SR
West Coast Vancouver Island, B.C. (a ⇒ a)	25	6.0	0.83	0.21	1.6	SR
Coho salmon (*Oncorhynchus kisutch*)						
Minter Creek, Washington (a ⇒ s)	10	14.2	0.39	0.00	1.1	Count
Steelhead trout (*Oncorhynchus mykiss*)						
Keogh River, B.C. (s ⇒ a)	7	5.7	1.00	0.00	3.3	Count
Keogh River, B.C. (a ⇒ f)	7	5.6	1.00	0.00	3.4	MR and removal
Keogh River, B.C. (a ⇒ s)	7	5.6	1.00	0.33	1.2	MR and count
Sockeye salmon (*Oncorhynchus nerka*)						
Adams Complex, B.C. (a ⇒ a)	39	7,498.8	0.95	0.00	160.8	SR
Ayakulik, Kodiak Island, Alaska (a ⇒ a)	22	25.6	0.95	0.00	2.9	SR
Babine Lake, B.C. (s ⇒ a)	23	14.6	0.86	0.36	1.8	MR and count
Babine Lake, B.C. (f ⇒ s)	23	10.0	0.86	0.23	3.0	MR and count
Babine Lake, B.C. (a ⇒ s)	10	14.7	1.00	0.22	3.6	MR and count
Birkenhead River, B.C. (a ⇒ a)	39	33.0	0.95	0.05	1.4	SR
Black Lake, Alaska (a ⇒ a)	38	22.3	0.69	0.22	2.3	SR
Branch River, Alaska (a ⇒ a)	33	35.5	0.94	0.31	1.5	SR
Bristol Bay, Alaska (a ⇒ a)	45	13.1	0.98	0.00	2.5	SR
Chignik Lake, Alaska (a ⇒ a)	38	7.2	0.31	0.08	0.9	SR
Chilko Lake, B.C. (a ⇒ s)	44	88.2	1.00	0.00	3.5	Count
Chilko River, B.C. (a ⇒ a)	39	72.5	0.68	0.11	2.9	SR
Chilko River, B.C. (s ⇒ a)	41	29.6	0.65	0.03	3.5	Count
Chilko South End, B.C. (s ⇒ a)	14	485.1	1.00	0.15	8.3	Count
Columbia River (a ⇒ a)	19	126.3	0.50	0.00	1.2	SR
Early Stuart Complex, B.C. (a ⇒ a)	39	305.8	0.97	0.00	4.7	SR
Egegik River, Alaska (a ⇒ a)	32	8.3	0.95	0.13	2.0	SR
Egegik River, Alaska (a ⇒ a)	39	8.9	0.84	0.08	2.6	SR
Egegik River, Alaska (a ⇒ s)	12	4.0	0.64	0.36	1.4	SR
Frazer Lake, Alaska (a ⇒ a)	24	54.0	0.63	0.00	3.2	SR
Fulton River, B.C. (a ⇒ f)	28	25.3	0.70	0.22	1.3	Count
Fulton River, Channel 1, B.C. (a ⇒ f)	21	48.1	0.80	0.00	1.8	Count
Fulton River, Channel 2, B.C. (a ⇒ f)	17	6.3	0.94	0.62	1.1	Count
Gates Creek, B.C. (f ⇒ a)	16	741.2	0.80	0.00	6.9	Count
Horsefly River, B.C. (a ⇒ a)	39	27,562.1	1.00	0.05	714.8	SR
Igushik River, Alaska (a ⇒ a)	39	124.2	0.55	0.24	1.6	SR
Karluk River, Alaska (a ⇒ a)	62	8.7	0.66	0.56	1.3	SR
Karymaisky Spring, Kamchatka (a ⇒ f)	8	34.0	1.00	0.00	5.0	Count
Kasilof River, Alaska (a ⇒ a)	21	13.0	0.90	0.10	2.3	SR
Kenai River, Alaska (a ⇒ a)	21	27.1	1.00	0.20	2.5	SR
Kvichak River, Alaska (a ⇒ s)	23	77.3	0.82	0.05	3.9	Count
Kvichak River, Alaska (a ⇒ a)	38	107.2	0.95	0.14	7.6	SR
Lake Dalnee, Kamchatka (a ⇒ s)	12	7.6	0.55	0.27	1.3	Count
Lakelse Lake, B.C. (a ⇒ s)	8	14.8	0.86	0.14	1.8	Count
Late Nadina River, B.C. (f ⇒ a)	11	15.6	0.60	0.00	5.9	Count
Late Stuart Complex, B.C. (a ⇒ a)	38	18,441.8	0.92	0.16	27.9	SR
Little Kitoi Lake, Afognak Is., Alaska (a ⇒ s)	7	9.2	0.50	0.00	1.4	Count
Naknek, Alaska (a ⇒ a)	38	26.4	0.92	0.07	1.9	SR
Naknek-Kvichak Rivers, Alaska (a ⇒ a)	32	16.2	0.95	0.00	1.9	SR
Nushagak River, Alaska (a ⇒ a)	32	33.7	0.58	0.00	1.3	SR
Nuyakuk River, Alaska (a ⇒ a)	20	30.9	0.84	0.47	3.4	SR
Pinkut Channel, B.C. (a ⇒ f)	17	3.2	0.94	0.69	1.5	Count
Pinkut Creek, B.C. (a ⇒ f)	26	27.4	0.44	0.08	1.5	Count
Port John Lake, B.C. (a ⇒ s)	9	30.9	0.50	0.62	0.5	Count
Quesnel Lake, Fraser River, B.C. (a ⇒ f)	10	7,211.9	0.67	0.00	2.7	Acoustics

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Red River, Alaska (a ⇒ a)	23	22.8	0.95	0.00	3.1	SR
Rivers Inlet, B.C. (a ⇒ a)	42	9.8	0.98	0.77	1.0	SR
Shuswap Lake, Fraser River, B.C. (a ⇒ f)	14	256.0	0.62	0.23	2.7	Acoustics
Skeena River, B.C. (a ⇒ a)	39	16.0	0.87	0.03	1.4	SR
Smith Inlet, B.C. (a ⇒ a)	10	2.8	0.72	1.00	1.3	SR
Stellako River, B.C. (a ⇒ a)	39	17.1	0.97	0.11	2.6	SR
Tahltan Lake, B.C. (a ⇒ f)	9	26.5	0.12	0.75	0.6	Count
Tahltan Lake, B.C. (a ⇒ s)	9	26.5	0.12	0.88	0.5	Count
Tahltan Lake, B.C. (a ⇒ a)	12	8.3	0.18	0.36	0.8	SR
Tally Creek, B.C. (a ⇒ f)	11	6.7	0.70	0.20	2.4	Count
Togiak River, Alaska (a ⇒ a)	14	9.0	0.85	0.62	1.3	SR
Togiak River, Alaska (a ⇒ a)	33	21.1	0.78	0.34	1.8	SR
Ugashik River, Alaska (a ⇒ a)	30	9.2	0.90	0.72	2.0	SR
Ugashik River, Alaska (a ⇒ a)	38	85.5	1.00	0.05	2.8	SR
Ugashik River, Alaska (a ⇒ s)	9	3.8	0.50	0.38	0.9	SR
Upper Pinkut Creek, B.C. (a ⇒ f)	9	3.4	1.00	0.75	1.2	Count
Weaver Creek, B.C. (a ⇒ a)	39	190.1	1.00	0.11	3.1	SR
Weaver Creek, B.C. (f ⇒ a)	26	16.4	1.00	0.44	1.9	Count
Wood River, Alaska (a ⇒ a)	40	12.9	0.38	0.03	1.5	SR
Chinook salmon (*Oncorhynchus tshawytscha*)						
Wild Canadian Coastwide (a ⇒ a)	26	2.1	0.28	0.88	0.9	SR
Atlantic salmon (*Salmo salar*)						
Bec-Scie, Canada (a ⇒ s)	5	2.5	1.00	0.50	1.5	Count
Ellidaar River, Iceland (a ⇒ a)	37	7.7	0.25	0.69	1.0	Count
Girnock Burn, Scotland (a ⇒ p)	9	5.2	0.25	0.00	1.3	Count
Little Codroy River, Canada (a ⇒ s)	7	16.6	1.00	0.00	1.5	Count
Margaree River, N.S., Canada (a ⇒ a)	37	13.3	0.94	0.22	1.4	Count
Miramichi River, N.B., Canada (a ⇒ p)	13	5.7	0.92	0.00	1.8	Count
Pollett River, Canada (a ⇒ s)	8	28.7	1.00	0.71	2.4	Count
Restigouche River, Canada (a ⇒ p)	11	6.8	0.50	0.20	1.6	Count
River Bush, Northern Ireland (a ⇒ f)	12	4.5	0.27	0.00	0.8	Count and electrofishing
River Bush, Northern Ireland (a ⇒ s)	17	4.5	0.56	0.00	1.1	Count
Shelligan Burn, Section D, Scotland (f ⇒ a)	6	12.0	0.20	0.00	0.9	Count
Tobique River, Canada (a ⇒ a)	9	57.8	0.75	0.00	1.7	Count
Trinite, Canada (a ⇒ s)	8	2.9	1.00	0.57	0.9	Count
Western Arm Brook, Canada (a ⇒ a)	16	13.2	0.47	1.00	0.7	Count
Western Arm Brook, Canada (a ⇒ s)	15	13.2	1.00	0.14	1.4	Count
Brook trout (*Salvelinus fontinalis*)						
Hunt Creek, Michigan (a ⇒ f)	9	2.0	0.88	0.62	1.0	Count
Scorpaeniformes						
Scorpaenidae						
Pacific ocean perch (*Sebastes alutus*)						
Aleutian Is.	30	6.8	0.97	0.79	0.8	SPA
Gulf of Alaska	31	17.1	0.97	0.57	1.9	SPA
U.S. West Coast	29	7.6	0.86	0.07	2.9	SPA
Widow rockfish (*Sebastes entomelas*)						
W. U.S. + Canada	12	5.3	0.73	0.82	1.0	SPA
Redfish (*Sebastes marinus*)						
W. Greenland and Iceland	10	2.9	0.22	0.67	0.2	RV and SPA
Iceland	7	1.4	1.00	0.50	1.2	SPA
Redfish (*Sebastes mentella*)						
North East Arctic	23	19.6	0.91	0.05	3.9	SPA and RV
Squaliformes						
Squalidae						
Spiny dogfish (*Squalus acanthias*)						
Northwest Atlantic	21	11.2	0.85	0.05	1.3	RV

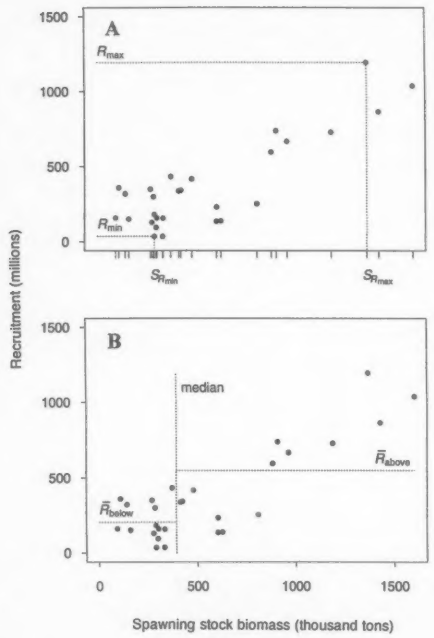

Figure 1

Illustration of the three nonparametric methods applied to spawner-recruitment data for Labrador–Newfoundland cod (Cod NAFO 2J3KL, Table 1). Here spawner abundance is measured as spawning stock biomass. (**A**) The maximum recruitment is R_{max} and the corresponding spawner abundance is S_{Rmax} which ranks 26th out of 28. Hence r_{max} = (26–1)/(28–1) ≈ 0.93. Similarly, the minimum recruitment is R_{min} and the corresponding spawner abundance is S_{Rmin} which ranks 8.5 out of 28 (since there is a tie). Hence r_{max} = (8.5 –1)/(28 –1) ≈ 0.28. (**B**) The mean recruitment below the median spawner abundance is $\overline{R}_{below}$ whereas the mean recruitment above the median spawner abundance is $\overline{R}_{above}$.

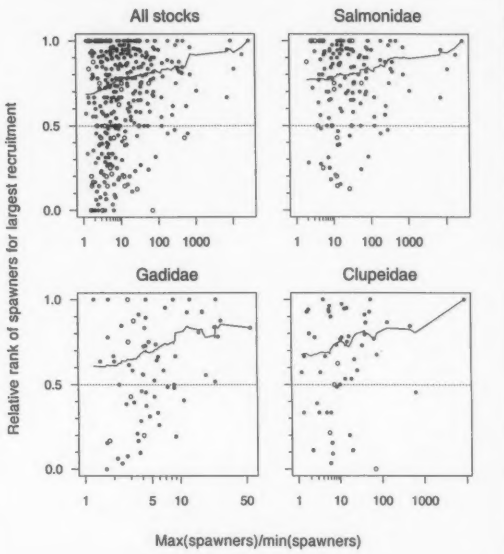

Figure 2

Scatter plots of the relative rank of spawner abundance for the highest recruitment versus the ratio S_{max}/S_{min} for all stocks and for three major families. Data points from series with fewer than 10 pairs of observations are shown as open circles. The horizontal axis has a logarithmic scale. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. To help summarize the data, we superimposed curves representing cumulative (from the right) weighted means on the plots in each figure.

tested the null hypothesis that the weighted mean relative rank is less than or equal to 0.5 versus the alternative hypothesis that it is greater than 0.5 . A sampled randomization test (Manly, 1991) of the null hypothesis of independence was easily performed. For the ith series, a random rank between 1 and n_i was selected, and the corresponding relative rank computed. This was performed for each series, and the weighted mean of the relative ranks was then computed. Repetition of this procedure (10,000 times sampling with replacement) gives an empirical null distribution of weighted mean relative ranks. If m of these 10,000 weighted means were greater than or equal to the observed weighted mean, we then assigned a one-sided P-value of $\frac{m+1}{10,001}$. The smallest one-sided P-value is thus $\frac{1}{10,001}$.

As with the cumulative weighted means, we took into account the varying reliability of the data based on the range of spawner abundance. Therefore, we performed significance tests beginning with the data having large values of S_{max}/S_{min} and progressively including data with smaller values of S_{max}/S_{min}.

For each family, the highest recruitment tends to occur when spawner abundance is high (Fig. 2). The cumulative weighted means never fell below 0.5 for any family. The cumulative weighted mean began on the right-hand side and accumulated to the left-hand side because we had greater confidence in the relative ranks obtained from time series having wide ranges of spawner abundance. Consequently, the value of the cumulative weighted mean on the extreme left-hand side encompassed all the data shown in the plot. Using the sample size as a weighting factor, we incorporated a greater confidence in the relative ranks obtained from long time series. The randomized test showed that the null hypothesis that

the weighted mean relative rank is less than or equal to 0.5 can be rejected for all stocks combined and for most of the taxonomic groups considered (Table 2A). In moving from left to right in the figure, the sample size used in the test decreased, whereas the reliability of the data (as gauged by S_{max}/S_{min}) increased. The tests were performed for all stocks, and separately for 3 major families. The overall trend of increase from left to right was due to the loss of power as the sample size used in the test decreased.

Hypothesis 2: Does the smallest recruitment occur when spawner abundance is low?

Next, we examined r_{min}, the relative rank of spawner abundance for the lowest recruitment (Fig. 1A). This time, $r_{min} = 0$ implies that the lowest recruitment occurs for the lowest spawner abundance, whereas $r_{min} = 1$ implies that the lowest recruitment occurs for the highest spawner abundance. As before, cumulative weighted means were calculated and a randomization test was performed.

The lowest recruitment tended to occur when spawner abundance was low (Fig. 3). Again, the pattern held for all stocks combined and for most of the taxonomic groups considered. The effect for the lowest recruitment appeared to be less than the effect for highest recruitment. The statistical significance of the results is usually less than 0.05, but there is a tendency for the significance to be reduced if the range of spawners is small (Table 2B).

Hypothesis 3: Is recruitment greater if spawner abundance is above rather than below the median?

Finally, for each spawner-recruitment series we asked whether the mean recruitment is the same when the spawner abundance is below or above the median. We split each spawner-recruitment series into two sections: the first section at or below the median spawner abundance, and the second section above the median spawner abundance. We then computed the mean recruitment for each section, which we denote as $\overline{R}_{above}$ and $\overline{R}_{below}$ respectively. When the mean recruitment is identical on both sides of the median spawner abundance, the ratio $\overline{R}_{above}/\overline{R}_{below}$ equals 1, or equivalently $\log(\overline{R}_{above}/\overline{R}_{below}) = 0$. A distribution-free test of this null hypothesis is the one-sample Wilcoxon signed rank test (Conover, 1980; Lehmann, 1975). We computed the ranks of the absolute values of the log ratios. The test statistic was given by the sum of the ranks of the positive log ratios. The logarithm was used because ratios of (for example) 1:2 and 2:1 would result in ties.

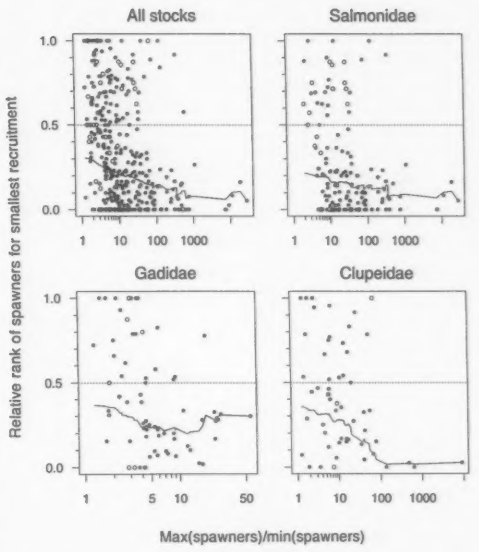

Figure 3

Scatter plots of the relative rank of the spawner abundance for the lowest recruitment versus the ratio S_{max}/S_{min} for all stocks and for three major families. See Figure 2 for explanation of data points, axis labels, and lines.

Our alternative hypothesis was that the median of the distribution of log ratios was greater than 0. For this one-sided test, in order to reject the null hypothesis (at the 5% significance level), we required at least 5 observations. When there were 25 or fewer log ratios, an exact probability for the test was computed; otherwise a normal approximation was used. Note that there were no ties in the absolute values of the log ratios.

This test is conservative because errors in the estimates of the range will bias the estimate of the slope downward (Judge et al., 1984). The ratio of the mean recruitment above the median level of spawners to that below, $\overline{R}_{above}/\overline{R}_{below}$, is greater than 1 for all families if the range of observed spawners is large (Fig. 4). For narrow ranges of spawner data, the ratio is closely clustered. When the data are grouped taxonomically, the pattern holds. The Wilcoxon signed rank test shows that the null hypothesis that the median of the distribution of $\overline{R}_{above}/\overline{R}_{below}$ is 1 can be rejected for all stocks combined and for most of the taxonomic groups considered.

Taxonomic variation

The Clupeidae show strong evidence of greater recruitment at large spawner-abundance levels. This

Table 2

Observed levels of significance for tests based on the data shown in Figure 2 (**A**) in Figure 3 (**B**), and in Figure 4 (**C**). The tests were conducted by using the data with $S_{max}/S_{min} \geq 1$, 2, 5, 10, 50, and 100. As this lower limit increases, the reliability of the data improves; however, the number of samples (shown in parentheses) decreases, thereby decreasing the power of the test. Empty cells indicate that there were no observations with the specified values of S_{max}/S_{min}. For populations within the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted as follows: a = adults (or eggs); f = fry; s = smolt; and p = parr. They are shown in the table with an arrow notation so that "a ⇒ f" means spawners were adults and recruits were fry or smolts.

A *P*-values corresponding to Figure 2 from one-sided randomization tests with 10,000 samples (with associated numbers of data sets in parentheses). The null hypothesis is that the weighted mean relative rank is less than or equal to 0.5. The alternative hypothesis is that the weighted mean relative rank is greater than 0.5.

	S_{max}/S_{min}											
Group	≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	< 0.0001	(55)	0.0002	(48)	0.0001	(40)	< 0.0001	(26)	0.0044	(9)	0.014	(4)
Herring	0.0007	(37)	0.0018	(30)	0.0006	(25)	< 0.0001	(16)	0.017	(5)	0.04	(3)
Sardine	0.18	(7)	0.18	(7)	0.31	(6)	0.2	(5)	0.28	(2)	0.16	(1)
Gadidae	0.004	(68)	0.0025	(61)	0.0003	(28)	< 0.0001	(13)	0.19	(1)		
Cod	0.023	(23)	0.014	(21)	0.024	(11)	0.0042	(5)	0.19	(1)		
Haddock	0.012	(9)	0.012	(9)	0.028	(6)	0.021	(5)				
Merluccius	0.043	(12)	0.047	(9)	0.0082	(4)	0.074	(2)				
Pollock or saithe	0.74	(6)	0.78	(5)	0.49	(2)						
Percidae	0.34	(9)	0.25	(8)	0.33	(5)	0.32	(4)	0.19	(2)	0.19	(2)
Scombridae	0.024	(9)	0.025	(8)	0.06	(6)	0.26	(4)	0.14	(1)		
Sparidae	0.23	(6)	0.23	(6)	0.008	(3)	0.24	(1)	0.24	(1)	0.25	(1)
Pleuronectidae	0.63	(19)	0.63	(17)	0.21	(4)	0.079	(3)				
Plaice	0.63	(8)	0.53	(7)	0.36	(1)	0.36	(1)				
Soleidae	0.45	(7)	0.45	(7)	0.13	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.0007	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	0.0001	(18)	0.0018	(9)
(a ⇒ f)	0.0098	(11)	0.0094	(11)	0.0091	(11)	0.017	(10)	0.15	(5)	0.067	(3)
(f ⇒ a)	0.023	(6)	0.022	(6)	0.041	(5)	0.059	(4)	0.46	(1)	0.45	(1)
Chum salmon	0.0092	(8)	0.0082	(8)	0.049	(5)	0.29	(3)	0.074	(1)	0.074	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	< 0.0001	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	< 0.0001	(11)	< 0.0001	(8)
(a ⇒ f,s)	0.0009	(21)	0.0014	(21)	0.0042	(17)	0.01	(13)	0.012	(4)	0.28	(2)
(f,s ⇒ a)	0.007	(6)	0.0079	(6)	0.008	(6)	0.0081	(6)	0.032	(2)	0.03	(2)
Atlantic salmon	0.065	(15)	0.068	(15)	0.091	(11)	0.0055	(7)	0.33	(1)		
Scorpaenidae	0.0007	(7)	0.0017	(6)	0.0005	(5)	0.012	(2)				

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relationship clearly holds for herring, whereas the evidence for sardines is not as strong.

The Gadidae, and particularly cod, show strong evidence for all three hypotheses. Haddock show strong evidence for the first two hypotheses, and weak nonsignificance for the third. The hakes of the genus *Merluccius*, show strong evidence for the hypothesis that strong year classes result from relatively high spawner abundance, fair evidence that the mean recruitment is greater for larger spawner abundances, and no evidence for the second hypothesis, except if there is a wide range of spawner abundances.

There is a relatively small range in observed spawner abundances for pollock, known as "saithe" in the eastern Atlantic. Given the narrow range of observed spawner abundances, there is evidence against the first hypothesis, some evidence for the second hypothesis, and no evidence for the third. An examination of the spawner recruitment curves for this species shows stronger evidence for overcompensation, i.e. reduced recruitment at high spawner abundances, than for any other group (see plots in Myers et al., 1995b). This species appears to be more cannibalistic than other Gadidae. Whiting, which is also highly cannibalistic, shows a similar narrow

Table 2 (continued)

B *P*-values corresponding to Figure 3 from one-sided randomization tests with 10,000 samples (with associated numbers of data sets in parentheses). The null hypothesis is that the weighted mean relative rank is greater than or equal to 0.5. The alternative hypothesis is that the weighted mean relative rank is less than 0.5.

	S_{max}/S_{min}											
Group	≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	0.0004	(55)	0.0003	(48)	0.0002	(40)	0.0004	(26)	0.0003	(9)	(4)	
Herring	0.0021	(37)	0.0014	(30)	0.0002	(25)	0.0002	(16)	0.0011	(5)	(3)	
Sardine	0.5	(7)	0.52	(7)	0.59	(6)	0.49	(5)	0.15	(2)	0.032	(1)
Gadidae	0.0007	(68)	0.0001	(61)	< 0.0001	(28)	0.0001	(13)	0.32	(1)		
Cod	0.0037	(23)	0.0042	(21)	0.0003	(11)	0.018	(5)	0.33	(1)		
Haddock	0.001	(9)	0.0006	(9)	0.0093	(6)	0.0053	(5)				
Merluccius	0.68	(12)	0.5	(9)	0.13	(4)	0.19	(2)				
Pollock or saithe	0.26	(6)	0.28	(5)	0.018	(2)						
Percidae	0.63	(9)	0.6	(8)	0.78	(5)	0.7	(4)	0.3	(2)	0.29	(2)
Scombridae	0.011	(9)	0.009	(8)	0.013	(6)	0.16	(4)	0.26	(1)		
Sparidae	< 0.0001	(6)	0.0001	(6)	0.0002	(3)	0.059	(1)	0.065	(1)	0.057	(1)
Pleuronectidae	0.11	(19)	0.068	(17)	0.03	(4)	0.01	(3)				
Plaice	0.21	(8)	0.089	(7)	0.18	(1)	0.19	(1)				
Soleidae	0.75	(7)	0.75	(7)	0.45	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.0002	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	< 0.0001	(18)	0.013	(9)
(a ⇒ f)	< 0.0001	(11)	< 0.0001	(11)	< 0.0001	(11)	< 0.0001	(10)	0.0001	(5)	0.0023	(3)
(f ⇒ a)	0.0005	(6)	0.0004	(6)	0.0001	(5)	0.0015	(4)	0.081	(1)	0.081	(1)
Chum salmon	0.0034	(8)	0.0042	(8)	0.0004	(5)	0.0025	(3)	0.15	(1)	0.14	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	< 0.0001	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	< 0.0001	(11)	< 0.0001	(8)
(a ⇒ f,s)	0.0005	(21)	0.0004	(21)	0.0001	(17)	0.0002	(13)	0.0002	(4)	0.049	(2)
(f,s ⇒ aa)	0.0055	(6)	0.0049	(6)	0.0042	(6)	0.0047	(6)	0.024	(2)	0.026	(2)
Atlantic salmon	0.026	(15)	0.026	(15)	0.099	(11)	0.11	(7)	0.11	(1)		
Scorpaenidae	0.36	(7)	0.36	(6)	0.33	(5)	0.24	(2)				

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range in observed spawner abundance and provides no evidence for our hypotheses.

Within the Perciformes, the freshwater Percidae, represented by perch of the genus *Perca*, and walleye and pikeperch of the genus *Stizostedion*, provide moderate evidence for the three hypotheses only when there is a very wide range of observed spawner abundance. However, for most of the marine species of the order Perciformes (e.g. the Scombridae, the mackerel and tunas, and the Sparidae, the sea breams) there was very strong evidence for all three hypotheses. One explanation for this pattern is that freshwater species for which we had data may have been less subject to overexploitation, but the question certainly deserves further study.

The order that showed the weakest amount of the relationship between the abundance of spawners and subsequent recruitment was the flatfish, i.e. the Pleuronectiformes. There was evidence for this relationship with both Pleuronectidae and Soleidae in all the tests for wider ranges in spawner abundance, i.e. the *P*-values in Table 2 were less than 0.5; however, these relationships were not statistically significant. The relatively weak relationship for flatfish may be caused by the strong density-dependent mortality for these populations (Myers and Cadigan, 1993; Iles, 1994). Furthermore, many of these populations have juvenile nursery grounds in regions where exploitation cannot take place. For these reasons, the range of spawner abundance has been relatively narrow, which reduces our ability to detect any relationship.

For the salmonids included in this analysis, large year classes almost always are associated with high spawner levels. This conclusion is true for the pink, chum, sockeye, and Atlantic salmon for each life-stage transition considered (Table 2). Our conclusion differs from that of Larkin (1977), who stated that for the Pa-

Table 2 (continued)

C *P*-values corresponding to Figure 4 from one-sample Wilcoxon signed-rank tests (with associated numbers of data sets in parentheses). The null hypothesis is that the median of $\log(R_{above}/R_{below})$, is less than or equal to 0. The alternative hypothesis is that the median is greater than 0. For this test, at least 5 observations were required to obtain a *P*-value less than 0.05.

	S_{max}/S_{min}											
Group	≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	0.0041	(55)	0.0068	(48)	0.0018	(40)	< 0.0001	(26)	0.0039	(9)	0.062	(4)
Herring	0.025	(37)	0.04	(30)	0.0031	(25)	0.0013	(16)	0.031	(5)	0.12	(3)
Sardine	0.15	(7)	0.15	(7)	0.16	(6)	0.062	(5)	0.5	(2)	0.5	(1)
Gadidae	0.0016	(68)	0.0011	(61)	0.00028	(28)	0.00061	(13)	0.5	(1)		
Cod	0.0017	(23)	0.00069	(21)	0.00098	(11)	0.031	(5)	0.5	(1)		
Haddock	0.33	(9)	0.33	(9)	0.22	(6)	0.16	(5)				
Merluccius	0.076	(12)	0.027	(9)	0.062	(4)	0.25	(2)				
Pollock or saithe	0.28	(6)	0.5	(5)	0.25	(2)						
Percidae	0.54	(9)	0.42	(8)	0.59	(5)	0.56	(4)	0.25	(2)	0.25	(2)
Scombridae	0.064	(9)	0.098	(8)	0.22	(6)	0.44	(4)	0.5	(1)		
Sparidae	0.047	(6)	0.047	(6)	0.12	(3)	0.5	(1)	0.5	(1)	0.5	(1)
Pleuronectidae	0.24	(19)	0.24	(17)	0.19	(4)	0.12	(3)				
Plaice	0.32	(8)	0.23	(7)	0.5	(1)	0.5	(1)				
Soleidae	0.53	(7)	0.53	(7)	0.25	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.00012	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	< 0.0001	(18)	0.002	(9)
(a ⇒ f)	0.00098	(11)	0.00098	(11)	0.00098	(11)	0.002	(10)	0.062	(5)	0.12	(3)
(f ⇒ a)	0.016	(6)	0.016	(6)	0.031	(5)	0.062	(4)	0.5	(1)	0.5	(1)
Chum salmon	0.012	(8)	0.012	(8)	0.031	(5)	0.12	(3)	0.5	(1)	0.5	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	0.00024	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	0.00049	(11)	0.0039	(8)
(a ⇒ f,s)	0.0031	(21)	0.0031	(21)	0.0064	(17)	0.02	(13)	0.062	(4)	0.25	(2)
(f,s ⇒ a)	0.016	(6)	0.016	(6)	0.016	(6)	0.016	(6)	0.25	(2)	0.25	(2)
Atlantic salmon	0.021	(15)	0.021	(15)	0.021	(11)	0.11	(7)	0.5	(1)		
Scorpaenidae	0.29	(7)	0.34	(6)	0.094	(5)	0.25	(2)				

cific salmon species of the genus *Oncorhynchus,* "recruitment is maximum at some intermediate stock size." The three hypotheses hold for the four salmon species in Table 2 and for all life-stage transitions.

Discussion

Could our results be an artifact of the necessary relationship between recruitment and subsequent spawner abundance? It has been argued that the observed relationships between spawners and recruitment is a by-product of the high autocorrelations present in some spawner and recruitment series. Consider a simple example in which recruitment is unrelated to the spawner abundance but is completely determined by the environment. Let recruitment be a first-order autoregressive process with autocorrelation parameter ρ, i.e. the correlation of recruitment with lag t is ρ^t. For a semelparous species, or a heavily-exploited species with relatively little survival after reproduction, the amount of variance in recruitment that would be "explained" by this process is ρ^{2a}, where a is the age at maturity. For example, if the age at maturity is $a = 4$ and the autocorrelation in recruitment is $\rho = 0.4$, then only 0.066% of the variance would be explained by spawner abundance. Thus, this mechanism will be important only when there is high environmental autocorrelation in recruitment and low age at maturity. However, when we restricted our analysis to data series with estimated autocorrelation less than 0.4, the observed patterns remained (Fig. 5). Alternative cutoff values for the degree of autocorrelation produced similar results. We conclude that our results are not caused by autocorrelation in recruitment and the necessary relationship between recruitment and subsequent spawner abundance.

In each of our three tests, the hypothesis that there is no practical relationship between spawners and

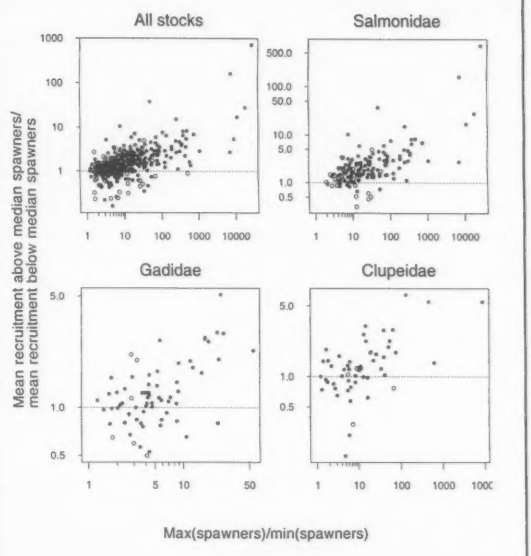

Figure 4

Scatter plots of the ratio $\overline{R}_{above}/\overline{R}_{below}$ versus the ratio S_{max}/S_{min} for all stocks, and for three major families. Data points from series with fewer than 10 pairs of observations are shown as open circles. Both axes have logarithmic scales. If spawner abundance and recruitment were independent, the distribution would be expected to have a median of 1.

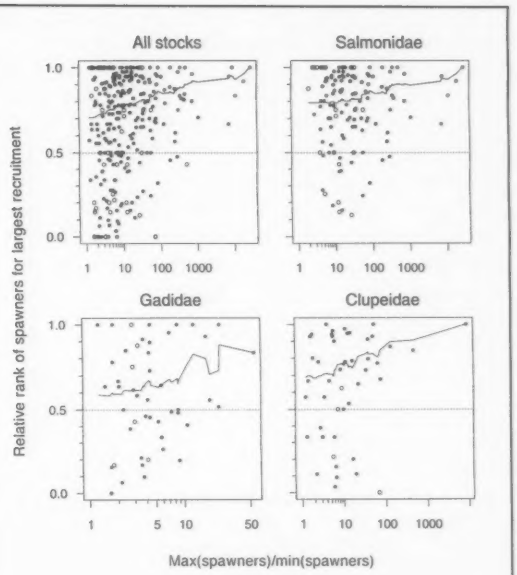

Figure 5

Test of the hypothesis that our results are caused by autocorrelation of recruitment. This scatterplot repeats the analysis shown in Figure 2 (the relative rank of spawner abundance for the highest recruitment versus the ratio S_{max}/S_{min}), except that populations with an autocorrelation in recruitment of 0.4 or greater are eliminated. Data points from series with fewer than 10 pairs of observations are shown as open circles. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. To help summarize the data, curves representing cumulative (from the right) weighted means are superimposed on the plots in each figure.

subsequent recruitment can be rejected. These conclusions hold for almost every species and family analyzed. These results also help to explain the widely-held belief that spawner abundance and recruitment are not related. When there is little variation in spawner abundance, no practical relation between spawners and subsequent recruitment may seem to be the case; however, wider ranges of spawner data reveal that the relationship holds. Sadly, many of the populations for which wide ranges of spawner data are available are those that have been fished to low levels, perhaps due, in part, to a rejection of spawner-recruitment relationships.

Our results are robust. We have considered three different approaches to our general question, and in each case the results are consistent with the hypothesis that recruitment is indeed linked to abundance of spawners. Errors in estimation of spawner abundance should have the effect of reducing the significance of our tests (Judge et al., 1984, chapter 5). For example, for our third question, errors in estimating spawner abundance would result in misclassifying observations and would reduce the magnitude of $\overline{R}_{above}/\overline{R}_{below}$. A second potential source of bias arises in the statistical analysis of spawner-recruitment relationships because the "independent" variable, spawners, is not independent of the interannual variation in the spawner-recruitment relationship. For a given spawning population, above-average recruitment tends to result in higher spawning populations, whereas below-average recruitment tends to result in lower spawning populations. This is called "time series bias" and causes the density-dependent mortality to be overestimated (Walters 1985, 1990; Myers and Barrowman, 1995). If this source of bias is important in our problem it will cause our conclusions to be conservative because the importance of density-dependent mortality will be overestimated, and thus recruitment would appear to be less positively related to spawners.

Some, who are not familiar with the fisheries literature, may consider our analysis unnecessary because the results seem obvious. However, the results

are not obvious and are not consistent with many claims that have been based on much less extensive, and less systematic, analyses. If a population is "managed" such that spawner abundance is reduced to low levels, the manager should not be surprised to observe the smallest recruitment ever recorded.

Are our results of practical importance for the management of fish populations? We believe the answer is clearly "yes." The simple observation that recruitment is generally lower at lower spawner abundances implies that recruitment overfishing is a pervasive problem among heavily exploited fish populations. The collapse of many of the fish stocks in the world, e.g. cod in eastern Canada (Myers et al., in press), can be at least partially blamed on reduced recruitment associated with reduction in spawner abundance.

We conclude that fish populations should be managed so as to maintain sufficient spawner abundance to yield high recruitment. Recruitment overfishing appears to be a common problem.

Acknowledgments

We thank the hundreds of assessment biologists whose hard work made this meta-analysis possible. We thank J. Hoenig, J. Hutchings, G. Mertz, N. Shackell, and W. Warren for advice and are grateful for financial assistance from the Northern Cod Science program.

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Abstract.—The spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific was studied by examining ovaries and testes collected from longline vessels operating in the waters off New Caledonia (21°–23°S, 164°–166°E) and Tonga (16°–29°S, 171°–177°W), January 1990 to February 1992. The monthly change in GSI values and mean oocyte diameters indicated that albacore are annual spawners, with most spawning limited to the austral summer months from November to February. Asymmetry in weight of, but not in the reproductive development of, the left and right gonad pairs was apparent in samples from the two collection sites; most right ovaries and testes were heavier and larger than those on the left side.

Spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific Ocean

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Albacore, *Thunnus alalunga*, are distributed throughout the Pacific in temperate and tropical waters. The North and South Pacific populations are considered to be separate stocks because 1) catch rates for these two populations are extremely low in the equatorial region, 2) the two populations have nonoverlapping spawning areas and different spawning seasons, and 3) there is no evidence that albacore tagged in the North Pacific move to the South Pacific (Lewis[1]). In the South Pacific, albacore are found from the Equator to 50°S latitude and from the surface to depths of 300 m (Yoneta and Saito, 1973). South Pacific albacore generally are considered to reach sexual maturity in the size range of 85 to 90 cm fork length [FL] (Ueyanagi, 1957; Otsu and Hansen, 1962), when they are usually between 6 and 8 years old (Labelle et al., 1993).

Two major fisheries target albacore in the South Pacific: a longline fishery concentrating on adult fish (80–110 cm) in tropical and subtropical waters (10°–30°S) throughout the year and a surface troll fishery targeting subadults (50–80 cm) in temperate waters (30°–40°S) during the austral summer (Lewis[1]; Rensink[2]). An area of research that was recognized by the second South Pacific Albacore Research (SPAR) workshop as needing further work was delineation of the spawning seasonality of albacore in the South Pacific. A sampling and histological project was organized by the Tuna and Billfish Assessment Programme (TBAP) of the South Pacific Commission (SPC) and the Southwest Fisheries Science Center (SWFSC) to provide a better understanding of albacore reproduction in the South Pacific. Because adult albacore at various stages of reproductive development were needed, sampling was limited to the longline fishery.

The purpose of our study is to report on the spawning seasonality of albacore in the South Pacific Ocean by using oocyte development and gonadosomatic indices as indicators of spawning activity.

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* Deceased.

[1] Lewis, A. D. 1990. South Pacific albacore stock structure: a review of available information. Third South Pacific albacore research workshop; Noumea, New Caledonia, 9–12 October 1990, Working Paper 5, 13 p. South Pacific Commission, B.P. D5, Noumea Cedex, New Caledonia.

[2] Rensink, G. 1991. Summary of the 1989–90 U.S. South Pacific albacore fisheries data. Southwest Fish. Sci. Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038. Admin. Rep.14:1–21.

Materials and methods

Albacore were sampled from the catches of two longline vessels: a Japanese–New Caledonia joint-venture with longliners fishing in New Caledonia waters (21°–23°S, 164°–166°E) and unloading in Noumea, and 2) the Tonga government-owned longliner, MV *Lofa*, operating in Tonga waters (16°–29°S, 171°–177°W) (Fig.1). These sampling arrangements were selected because these vessels fished throughout the year in known spawning areas. Fishing operations took place during daylight and standard commercial longline gear was used.

Sampling was designed to cause minimum disturbance to commercial operations while providing adequate samples and data. For both sampling operations, sex, fork length (to the nearest centimeter), and gonad weight (to the nearest g, New Caledonia [females]; or to the nearest 5 g, Tonga [females and males]) were measured. In waters near New Caledonia, ovaries from each 10-cm size class (70–79 cm, 80–89 cm, 90–99 cm, and 100–110 cm) were collected each collection day, but actual quantities were dependent on the landings from the commercial operation. However, in waters near Tonga, ovaries were collected only from albacore in the 80–89 cm size class because of sampling limitations. Sampling in waters near New Caledonia was done once a week, May 1990 to February 1992, whereas sampling near Tonga occurred on every second set of the longline during January 1990 to February 1992.

In New Caledonia and aboard *Lofa*, gonads were removed from the gut cavity of albacore and identified as male or female. Each pair was separated into a left and right section and weighed fresh to the nearest 1 g in New Caledonia and to the nearest 5 g on *Lofa* for size comparison. Weights of fresh gonads included the weight of the associated fatbody.

A total of 1,105 albacore were examined and measured (300 females, 799 males, 6 undetermined); of this number, 246 pairs of ovaries and 444 pairs of testes were weighed fresh (Table 1). A subset of 150 ovaries were collected from female albacore in various stages of development for histology. A greater percentage of the ovaries collected came from New Caledonia because ovary collections from waters near Tonga were limited to ovaries from albacore in the 80–89 cm FL size range. In the laboratory, the ovary was removed from a formalin fixative, patted dry, and weighed to the nearest 0.1 g. The associated fatbody was then removed and the ovary reweighed without the fatbody; these values were then used to calculate the gonadosomatic index (GSI). Male albacore testes were not collected for histological study from either site.

Histological processing was done by staff at the Maas Diagnostic Laboratories who followed the

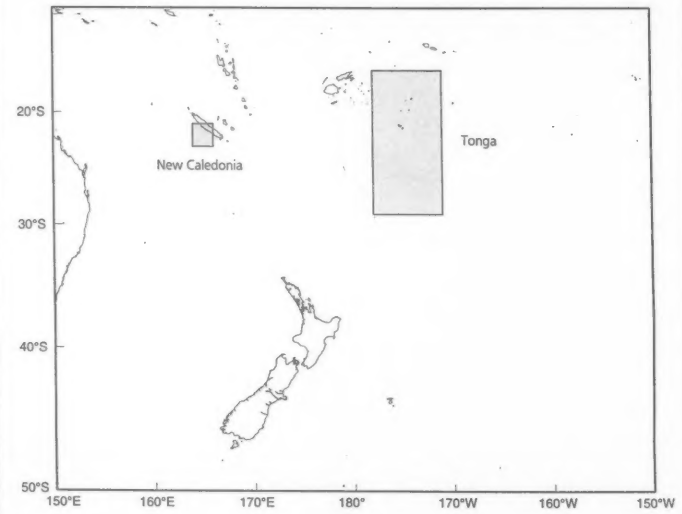

Figure 1

Sampling areas for albacore, *Thunnus alalunga*, in the South Pacific Ocean near New Caledonia and Tonga from 1990 to 1992.

Table 1

Summary of albacore gonads sampled in the South Pacific, January 1990–February 1992. Undeter. = undetermined.

Site	Sampling period	Sex	Number of albacore examined	Number of gonads weighed	Number of ovaries collected
New Caledonia	May 1990–February 1992	Female	108	104	105
		Male	239	0	0
		Undeter.	6	0	0
Tonga	January 1990–February 1992	Female	192	142	45
		Male	560	444	0

methods described in Hunter et al. (1986). A cross section of the ovary was taken from the middle region of the ovary, dehydrated, embedded in paraffin, sectioned at 7 μm, and stained with Harris's hematoxylin followed by eosin counterstain. The slides were examined with a compound microscope to determine the stage of ovarian development (as characterized by the presence or absence of yolk, lipid vesicles, hydrated oocytes, and postovulatory follicles) and were classified as early developing (unyolked), late developing (partially yolked), or advanced (fully yolked) (Schaefer, 1987). A second cross section of ovarian tissue was taken from the outer edge of the ovary to the lumen. This sample was placed in 33% glycerol for 10 to 20 minutes to separate the oocytes from the ovarian connective tissue (Hunter et al., 1986). The separated oocytes were then measured to 0.01 mm to determine the average size of the most developed stage of oocytes in each ovary; this was done by measuring the diameter of 20 oocytes in the sample as described by Schaefer (1987). The mean diameter of the most advanced stage of oocytes was plotted against months to examine the seasonal trend of maturity (Fig. 2). Oocyte diameter and developmental stage of the ovaries were examined to see if differences in weight between the right and left sides of the ovary were associated with differences in the reproductive state.

The histological condition of the samples did not provide the resolution necessary to distinguish

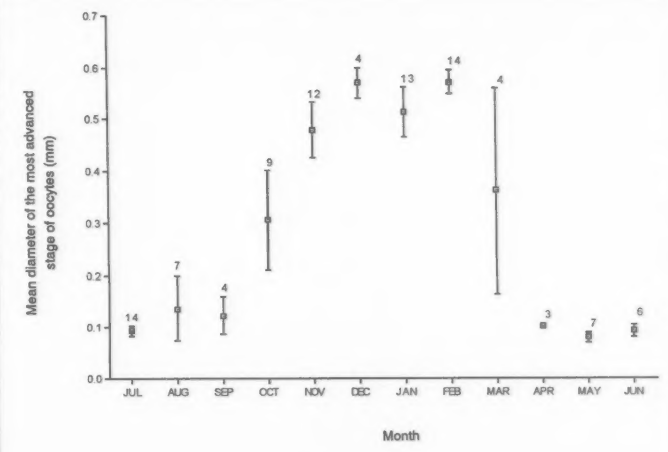

Figure 2

Monthly variation in mean diameter of the most advanced stage of oocytes for albacore, *Thunnus alalunga*, sampled from New Caledonia and Tonga, 1990 to 1992 (±2 standard errors; n=97). Numbers above error bars indicate the sample size for each month.

postovulatory follicles from preservation artifacts. Because of the time between capture and preservation, significant amounts of atresia occurred. The atresia limited the usefulness of the ovary sections because postovulatory follicles could not be distinguished from atretic conditions and histological materials.

Gonadosomatic indices (GSI) were calculated from the ovarian samples collected from New Caledonia and Tonga by using the formula of Kume and Joseph (1969):

$$GSI = 10^4 W/L^3,$$

where W = total gonad weight in grams minus fatbody and L = fork length in centimeters. The GSI was calculated only for those females whose ovaries were collected and processed in the laboratory. The critical GSI value was determined to be 1.7 according to the definition of maturity by Cayré and Farrugio (unpubl. data),[3] the value for which 100% of the females display an advanced mode of oocyte development (>0.3 mm) (Fig. 3).

[3] Cayré, P., and H. Farrugio. 1983. Biologie de la reproduction du listao *Katsuwonus pelamis* de l'Océan Atlantique. Doc. SKJ. Conf./83/12, présenté à la réunion de clôture du Programme International de Recherches sue le listro Atlantique, Teneriffe (Espagne), juin 1983, 62 p.

Results

Length-frequency distributions of sampled albacore

Length and sex data were collected on 1,105 albacore in the South Pacific. Size frequencies differed between males and females in both the New Caledonia and Tonga sites (Fig. 4, A and B). Male albacore had two size modes, 8–91 cm FL and 100–102 cm FL (Fig. 4, A and B). The relative strength of the modes differed at each sampling site. Female albacore from New Caledonia had a single mode, 86–92 cm FL (Fig. 4A), whereas females from Tonga possibly displayed two size modes, 87–89 cm FL and 92–96 cm FL (Fig. 4B). Few females over 100 cm FL were collected in either the New Caledonia or Tonga samples.

Male albacore were encountered more often than female albacore (Fig. 4, A and B). Male albacore accounted for 68.9% of the samples from New Caledonia and for 74.5% of the samples from Tonga (Table 1).

Oocyte development

The most advanced stage of oocytes collected during the austral winter months was the unyolked oocytes

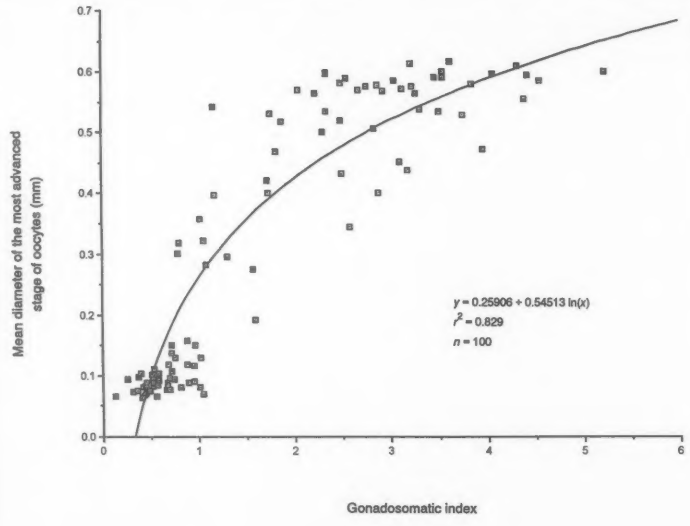

Figure 3

Relationship between the mean diameter of the most advanced stage of oocytes and the gonadosomatic index of female albacore, *Thunnus alalunga*, sampled from New Caledonia and Tonga, 1990 to 1992.

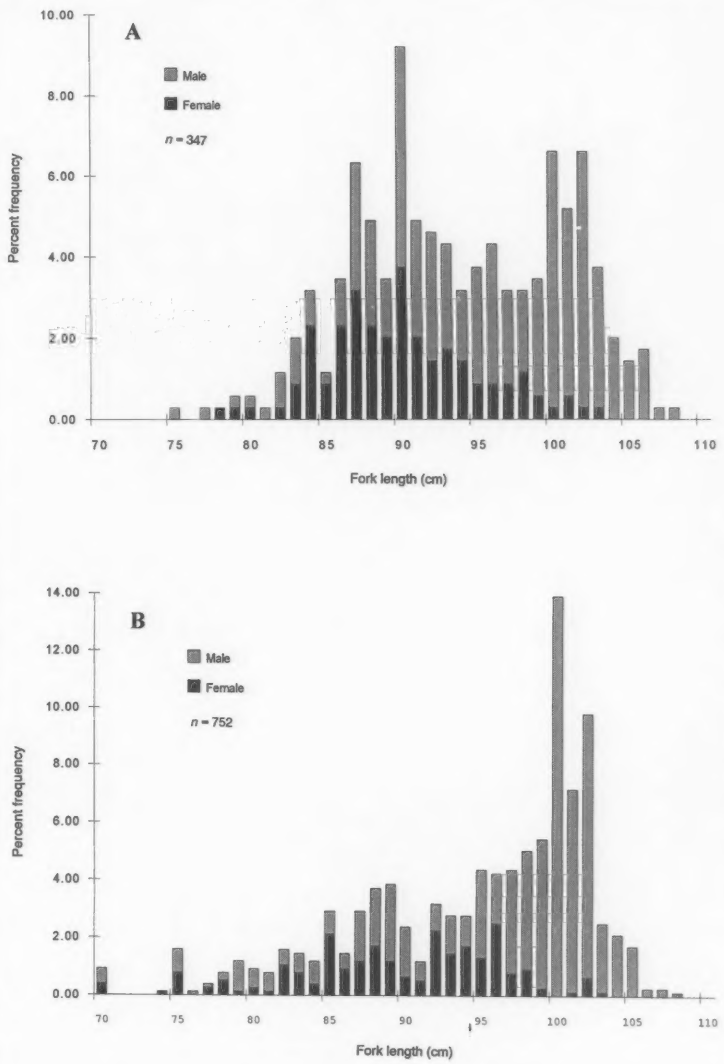

Figure 4

(**A**) Length-frequency distribution of albacore, *Thunnus alalunga*, sampled from New Caledonia, January 1990–February 1990; (**B**) Length-frequency distribution of albacore, *Thunnus alalunga*, sampled from Tonga, January 1990–February 1990.

with a mean diameter near 0.1 mm (Fig. 2). Between September and December, the number of albacore with partially yolked or fully yolked oocytes increased rapidly, and mean monthly oocyte diameters progressed from 0.12 mm to 0.57 mm (Fig. 2). Albacore with fully yolked oocytes were found from the summer months through March. No hydrated ovaries were observed in either the New Caledonia or the Tonga samples. By April, the most advanced-stage oocytes were resting-state oocytes with a mean diameter of 0.1 mm for all samples (Fig. 2).

A correlation exists between the most advanced stage of oocytes and GSI, as indicated by the positive coefficient of determination, $r^2 = 0.829$ (Fig. 3).

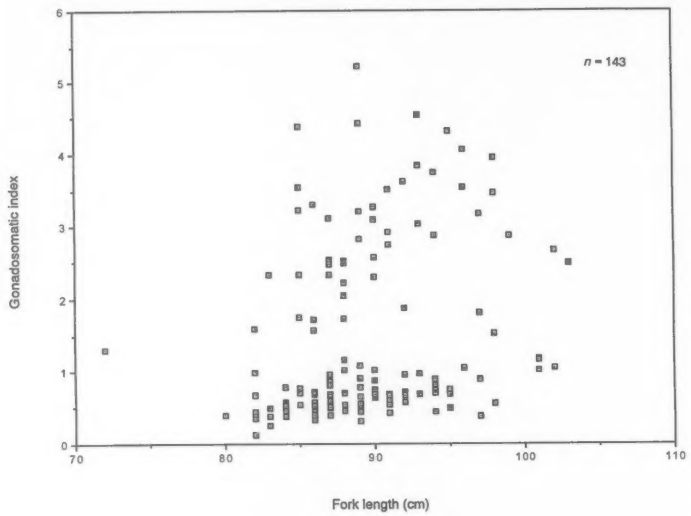

Figure 5

Gonadosomatic index values for female albacore, *Thunnus alalunga*, versus fork length, sampled from New Caledonia and Tonga from 1990 to 1992.

Gonadosomatic index

Because albacore gonads often have a fatbody attached, only those samples processed at the Southwest Fisheries Science Center (SWFSC), with the fatbody removed, were used in calculating GSI. The weight of the fatbody was found to compose an average of 4.4% of ovarian weight, from 0.0% to 31.6% in the samples sent to the SWFSC for processing. Because of the large variability in the weight of the fatbody, we decided not to attempt any corrections for fatbody presence but to use only the weight of ovaries measured in the laboratory. The relationship between GSI and fork length of sampled female albacore is shown in Figure 5.

In this study, a GSI of 1.7 was used as the critical GSI value, delimiting the point at which 100% of the females in our sample displayed an advanced stage of oocyte development (>0.3 mm)(Fig. 3). GSI values of 1.6 (Kikawa, 1959, 1966), 2.0 (Shung, 1973; Koido and Suzuki, 1989), and 2.1 (Kikawa, 1962) have been used to indicate group maturity of different species of female tunas. Female albacore appear to be capable of achieving this level of ovarian maturity and therefore of spawning once they reach 82 cm FL (Fig. 5). Evidence of spawning, as indicated by the presence of residual hyaline oocytes, was found in an 85-cm-FL albacore with a GSI of 2.8 and a mean maximum oocyte diameter of 0.57 mm. The largest GSI measured was 5.2 for a 89-cm female captured in Tonga in November. The weight of its ovary was 368.3 g, and the mean oocyte diameter of its most advanced oocytes was 0.60 mm.

The mean monthly GSI's of females show that peak reproductive development (GSI>1.7) occurs in the austral summer months, November–February (Fig. 6). The first indication of maturation was observed in October, when three of 15 albacore sampled were found to have GSI's greater than 1.7. These three had partially and fully yolked oocytes in the 0.35–0.54 mm size range. The first large increase in mean monthly GSI value occurred in November, when the mean GSI increased to 3.2 (Fig. 6). The largest monthly GSI, a mean of 3.3, occurred in February (Fig. 6). In March, the mean GSI declined to 1.2, although a small number of females still exhibited some spawning activity as indicated by females with high GSI values and late developed ovaries with oocyte diameters greater than 0.3 mm. The mean GSI then dropped to a resting level, close to 0.5, for the austral autumn and winter months.

Gonadal asymmetry

The right gonad was found to be heavier than the left in 80.0% of the females examined, and in 98.6% of the males (Table 2). In terms of collection sites,

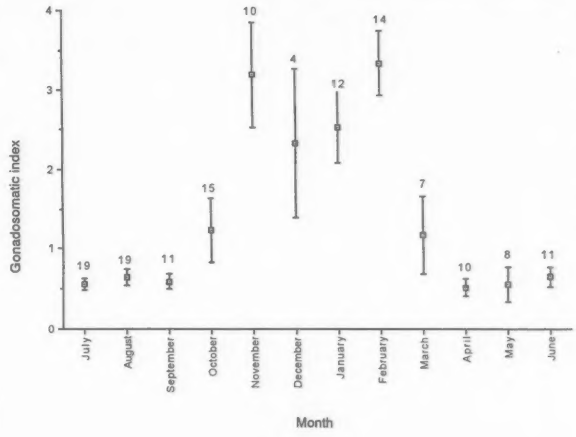

Figure 6

Mean monthly gonadosomatic index values for female albacore, *Thunnus alalunga*, by month, sampled from New Caledonia and Tonga from 1990 to 1992 (±2 standard errors; n=140). Numbers above error bars indicate sample size for each month.

the difference in females was less pronounced in New Caledonia (55.8%) than in Tonga (95.1%).

The left and right ovaries showed no significant difference in oocyte diameters between the left and right ovaries in the paired t-test ($T_{0.05(2),83}$=1.902). Only one of the 150 ovary pairs examined revealed a difference in maturity stages, with the left and smaller ovary being classified as developing and the right and larger as late developing.

Discussion

Our data indicate that albacore caught near New Caledonia and Tonga are seasonal spawners, spawning mainly during the austral summer months, November–February. This supports the work on albacore reproduction in the South Pacific by Otsu and Hansen (1962). Nishikawa et al. (1985) and Ueyanagi (1969) analyzed larval data and determined that spawning was greatest in spring and early summer (October–December). Few larval surveys, however, were undertaken later in the season, January–March in the spawning area (see Fig. 37 in Nishikawa et al., 1985). It should be noted that albacore larvae are reported to occur south of 10°S in the South Pacific for all months except July–September (Nishikawa et al., 1985), indicating that spawning may be protracted. Leis et al. (1991) found high concentrations of albacore larvae near the islands of French Polynesia (14°–17°S) in January and February, corresponding to the period of peak reproduction period observed in this study.

Table 2

Asymmetry in gonad weight of albacore sampled from New Caledonia and Tonga, 1990–92.

Gonad weight (g)	New Caledonia female	Tonga female	Tonga male
Right> Left	55.77%	95.10%	98.60%
Right = Left	17.31%	4.90%	1.10%
Right < Left	26.92	0.00%	0.20%
n	104	142	444
$\bar{x}$	9.5	19.3	12.9
SD	41.6	13.7	12.8
Range	–130, +160	0–100	–30, +105

From the distribution of larval and juvenile albacore, various authors have shown that the spawning area of South Pacific albacore lies between 10° and 25°S (Otsu and Hansen, 1962; Nishikawa et al., 1985; Ishii and Inoue, 1956; Ueyanagi, 1969). In this study, most maturing albacore (i.e. with GSI's above 1.7) were taken between 20° and 23°S.

Both the New Caledonia and the Tonga GSI data support the view that female albacore reach maturity at a minimum length of around 82 cm (Fig. 5). Although, GSI values alone may not present a full

picture of gonadal activity, the similarity in trends of monthly values of GSI's and oocyte diameters (Figs. 2 and 6) suggests that either method can be used to determine spawning season for the samples as a group.

The length frequencies of male and female samples from New Caledonia and Tonga indicate sexually dimorphic size differences. Such dimorphism had previously been reported by Otsu and Sumida (1968). In yellowfin tuna, sexually dimorphic growth has been age verified, and males were found to represent the largest mode in fork lengths (Wild, 1986).

Gonadal asymmetry has been recorded in several fish species (Ovchinnikov, 1971; Sanwal and Khana, 1972) and was documented previously in albacore by Otsu and Uchida (1959) and Ueyanagi (1955). The former compared oocyte diameters from different areas of one pair of ovaries and found that differences existed between anterior and posterior regions of a single ovary but not between the sides. In contrast, Ratty et al. (1990) found that the smaller left testis of males from the temperate troll fishery was consistently more active than the larger right testis. We found no significant difference in the diameters of oocytes in left and right ovaries.

The absence of advanced and fully ripe ovaries in our samples is similar to the state of reproductive development of ovaries in other studies of albacore reproduction in the Pacific that have relied on longline fisheries as the main source of samples (Otsu and Uchida, 1959; Otsu and Hansen, 1962). As these authors have noted, albacore in, or close to, spawning condition are generally unavailable to the fishery, either because they have stopped feeding and will not take hooks or because they have moved beyond the range of gear. In order to capture the latter category of fish, both the New Caledonia longliners and the MV *Lofa* crew set and hauled their gear during daylight hours; it is possible, however, that albacore, like some other tunas, spawn at night (Hunter et al., 1986; Schaefer, 1996). In addition, albacore may pass rapidly through the mature and spawned stages of the cycle, as Hunter et al. (1986) found with skipjack tuna, and McPherson with yellowfin tuna (1991). Thus, there remain a number of key aspects of the reproduction of South Pacific albacore, such as spawning frequency, batch fecundity and length at 50% maturity, that require further investigation.

Acknowledgments

We are grateful to the many South Pacific Commission TBAP and Fisheries Programme staff who assisted in the collection of gonads and related data in New Caledonia. Special thanks are due to the radio operators and crew of MV *Lofa*, who, in the course of their normal duties, collected and weighed a considerable number of gonads. We also thank Tevita Finau Latu, Tongan Ministry of Fisheries, for coordinating sampling on *Lofa*. This paper has benefitted from discussions with colleagues at the Southwest Fisheries Science Center and South Pacific Commission, notably John Hampton and Marc Labelle of the South Pacific Commission and Norman Bartoo and David Au of the Southwest Fisheries Science Center.

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Immunologic methods for species identification of early life stages of lutjanid fishes from the western central Atlantic. Part I: Characterization of an interspecies protein

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Abstract.—A 66 kDa glycoprotein selected from SDS-PAGE gel profiles of soluble extracts of *Lutjanus griseus* was purified by Fast Protein Liquid Chromatography technology. A polyclonal antiserum produced to the single-chained glycoprotein was tested with 14 other lutjanid extracts in Western blots and produced 3 different patterns: strong reactions with *L. jocu* and *L. apodus;* weak reactions with *L. buccanella, L. synagris, L. analis, L. campechanus, Pristipomoides aquilonaris, Ocyurus chrysurus,* and *Apsilus dentatus;* no reactions with *L. vivanus, L. mahogoni, L. cyanopterus, Etelis oculata,* and the hybrid *L. synagris* × *O. chrysurus.* The anti-66 kDa antiserum also reacted strongly with soluble extracts of oocytes and juveniles of *L. griseus.* Adsorption of the IgG fraction of the antiserum with glutaraldehyde-insolubilized *L. apodus* extract resulted in an antiserum that remained strongly reactive with *L. griseus* extract but that was weakly reactive with *L. apodus* extract and negative with *L. jocu* extract in Western blots. The N-terminal amino acid sequence analyses of the first 10 residues of the purified 66 kDa proteins of *L. griseus* and *L. jocu* were approximately the same, but only 3 of 10 residues were the same with the purified proteins of *L. griseus* and *L. apodus.* Extracts of *L. apodus* contained 3 additional proteins that were not detected in extracts of *L. griseus* as determined by SDS-PAGE. This evidence for both interspecies and species-specific protein determinants is currently being used to produce species-specific polyclonal and monoclonal antisera for identifying species of lutjanid fishes at early life history stages.

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Eighteen species of snappers (Lutjanidae), representing 5 genera, are found in the western Atlantic Ocean (Robins et al., 1991). Species identification of the early life stages of snappers is incomplete because meristic characters are very similar or equivocal within the family. In addition, identification of morphological features requires a great deal of time and experience. Innovative studies are necessary for further species-specific identification of early life stages (eggs, larvae, and early juveniles) because information is available for only a few species and each exhibits a complex recruitment strategy (Richards et al., 1994). Lutjanids constitute one of the major predators of coral-grazing species, but the detrimental impact of overfishing and habitat loss from pollution and development is rapidly leading to an imbalance in the fragile equilibrium of the reef community. Thus, the ability to identify the early life stages of specific lutjanids is an important aspect of conservation measures.

Specific antibodies directed against a minor protein may be useful for species identification at the early life stages (Diano et al., 1992). In our study, starting with the development of biochemical methods to isolate a very pure antigen, we have produced a polyclonal antibody for prototypic studies of previously difficult or unapproachable questions of identification of early life history specimens of snapper. These methods and immunologic reagents have

wide versatility and applicability for current and future studies of early life history forms. The chromatographic purification and characterization of a 66 kDa glycoprotein from soluble extracts of *Lutjanus griseus* (Linnaeus), *L. jocu* (Schneider), and *L. apodus* (Walbaum) and the production of a specific polyclonal antiserum have generated evidence that the glycoprotein has both interspecies and species-specific epitopes. Further characterization of this and other lutjanid proteins, together with the production of both polyclonal and monoclonal antibodies for immunologic assays, may greatly facilitate future identification of lutjanids at any stage of their life history.

Materials and methods

Adult lutjanid specimens were obtained from local fishermen and skin divers, and species identification was carried out according to Robins and Ray (1986) and Robins et al. (1991).

Buffers and the methods for preparing soluble saline fish extracts are described in Schultz and Clarke (1995). In addition to *L. griseus*, the 13 species and one hybrid investigated here were the following: *L. jocu, L. apodus, L. vivanus* (Cuvier), *L. campechanus* (Poey), *L. analis* (Cuvier), *L. synagris* (Linnaeus), *L. mahogoni* (Cuvier), *Ocyurus chrysurus* (Bloch), *L. buccanella* (Cuvier), *Pristipomoides aquilonaris* (Goode and Bean), *Etelis oculata* (Valenciennes), *L. cyanopterus* (Cuvier), *Apsilus dentatus* (Guichenot), and the hybrid *L. synagris* × *O. chrysurus*. Separate extracts were prepared in 300 mL of buffer with approximately 30 g of tissue from gutted legal-size adult fish. The soluble, clear extract was concentrated by ultrafiltration (M_r 10,000 membrane, Amicon Corp., Danvers, MA) at 4°C until the OD_{280} exceeded 10. Also extracted were 1) gutted *L. griseus* juveniles with a total weight of 0.6 g and 2) *L. griseus* female gonads with oocytes, weighing approximately 3.5 g. Juveniles were collected from Biscayne Bay, Florida.

Two different antisera were produced in adult female goats according to the innoculation schedule of Schultz and Clarke (1995). The first was a polyvalent antiserum (anti-GSE) raised against *L. griseus* whole fish extract (14.1 mg protein/mL). The second antiserum (anti-66 kDa) was produced by using the 66 kDa protein (0.32 mg/mL) purified from *L. griseus* saline extracts (see below).

The γ-globulin fraction of anti-GSE and anti-66 kDa sera was isolated by 33% ammonium sulfate (A.S.) precipitation at 25°C (Stelos, 1967) and was further purified as IgG by DEAE-Sephacel (Pharmacia BioTech, Uppsala, Sweden) column chromatography in 10 mM NaPO4/50 mM NaCl, pH 7.4. The IgG-rich fractions were concentrated by ultrafiltration as above.

To eliminate background interference when anti-GSE was used as the primary antiserum in Western blots, it was necessary to biotinylate the IgG fraction (Bayer and Wilchek, 1980). The biotin-conjugated anti-GSE IgG was recovered by Sephadex G-25 (Pharmacia BioTech) gel filtration in 5 mM NaPO4/150 mM NaCl, pH 7.5 (PBS) and the biotin-protein ratio was 56 nmol of biotin per nmol of IgG (Green, 1965).

Soluble extracts of *L. mahogoni, L. apodus,* and *Eucinostomus gula* (silver jenny) were insolubilized with glutaraldehyde according to the method of Avrameus and Ternynck (1969), with 10 mg of glutaraldehyde per mg of soluble fish protein. Insolubilized *E. gula* was used previously to remove cross-reactivity with preimmune and immune goat sera and unrelated fish proteins (Schultz and Clarke, 1995).

The γ-globulin fraction of goat anti-66 kDa serum was adsorbed for 24 to 48 h at 4°C with 60 mg of insolubilized *E. gula* extract per mL γ-globulin, followed by 24 mg of insolubilized *L. mahogoni* extract (the 66 kDa protein was not detected in this species in Western blots). The IgG fraction of the adsorbed anti-66 kDa serum (anti-66 kDa IgG) was isolated by DEAE-Sephacel chromatography (see protocol above). This procedure removed all nonspecific activity.

Another portion of the γ-globulin fraction of anti-66 kDa serum was adsorbed with 100 mg of insolubilized *L. apodus* extract for 24 h per adsorption at 4°C in experiments to distinguish the 66 kDa proteins found in soluble saline extracts of *L. griseus, L. jocu,* and *L. apodus* (see Results section).

The buffers and conditions for ion exchange chromatography with the Fast Protein Liquid Chromatography (FPLC) system (Pharmacia Biotech, Uppsala, Sweden) as described in Schultz and Clarke (1995) were modified to include 10 mM EDTA in the column buffers. The sequence was that of Mono S cation exchanger followed by Mono Q anion exchanger.

Gel filtration on Sephacryl S-300 Superfine (Pharmacia Biotech) in PBS/10 mM EDTA, pH 7.5, was used to separate high molecular weight contaminants from the 66 kDa protein.

During purification procedures, protein concentration was monitored by absorbance at 280 nm. Purified proteins were dialyzed against PBS, pH 7.5, to remove EDTA, and the protein concentration was determined spectrophotometrically as described previously (Arnold et al., in press). Methods for electrophoresis in 10% (w/v) polyacrylamide gels with or without sodium dodecylsulfate (Laemmli, 1970), for Western blots (Towbin et al., 1979), and the molecu-

lar weight standards (Sigma Chemical) are described in Schultz and Clarke (1995).

Glycoproteins were identified on electroblots by using the method of O'Shannessy et al. (1987).

Results

The steps for purification of a 66 kDa protein from a soluble saline extract of *L. griseus* are shown in Table 1. Figure 1 depicts samples of each purification step in SDS-PAGE (gel A) and corresponding Western blots (gels B and C) leading to the highly purified protein. The protein was a trace component of the saline extract (arrow, A1) but was more concentrated with successive purification steps (A, 2–4). The steps of purification included *L. griseus* saline extract in lane 1, the A.S. (0.38 gm/mL extract) supernatant solution of the extract in lane 2, the 0.27 M NaCl eluate from a Mono S cation exchange column after

Table 1

Steps for the purification of *L. griseus* 66 kDa protein. FPLC = Fast protein liquid chromatography.

Procedure	Product
1 Puree fish, separate solid material by centrifugation	Clear extract
2 Solid ammonium sulfate fractionation (0.38 g/mL extract)	Supernatant fluid: elimination of most high molecular weight proteins in precipitate
3 FPLC: Mono S cation exchanger; gradient: 0 to 1.0 M NaCl, pH 5.0	Enriched 66 kDa protein eluted at 0.27 M NaCl
4 FPLC: Mono Q anion exchanger; gradient: 0 to 1.0 M NaCl, pH 7.5	Highly purified 66 kDa protein eluted at 0.32 M NaCl

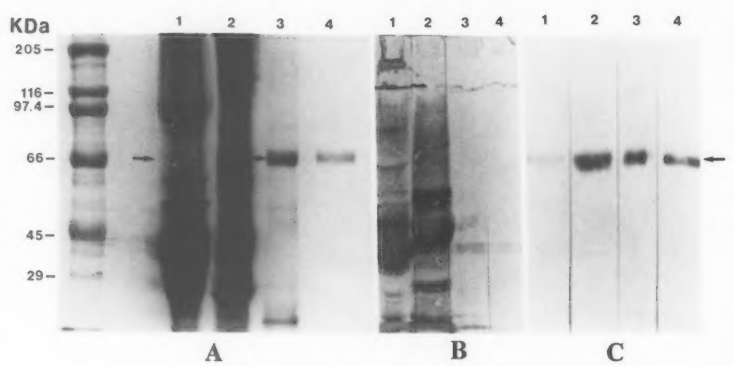

Figure 1

Samples from the purification steps of soluble *L. griseus* extract leading to the highly purified 66 kDa protein in lane 4. Gel (**A**) shows samples after SDS-PAGE stained with Coomassie brilliant blue. The corresponding Western blots were developed by using biotinylated goat anti-whole *L. griseus* antiserum (**B**) and goat anti-*L. griseus* 66 kDa protein IgG (**C**). Reference standard proteins (kDa) are shown in the stained gel. The arrows in gels A and C show the position of the 66 kDa protein. Numbered lanes denote the following: 1) whole *L. griseus* extract (235 µg total protein); 2) ammonium sulfate (0.38 g/mL extract) supernatant solution of *L. griseus* whole extract (228 µg); 3) eluate from Mono S cation exchange column (20 µg) after FPLC; and 4) eluate from Mono Q anion exchange column (0.32 µg) after FPLC. Note that the reaction of biotinylated goat anti-whole *L. griseus* antiserum with the 66 kDa *L. griseus* protein was not detected in B.

FPLC in lane 3, and the 0.32 M NaCl eluate of the highly purified 66 kDa protein from a Mono Q anion exchange column after FPLC in lane 4. Although the biotinylated goat anti-GSE antiserum reacted with many different proteins in the saline extract, it did not contain antibodies that were reactive with the trace 66 kDa protein in the Western blot (B, 1–4). In contrast, where the goat anti-66 kDa IgG was used, the protein was weakly positive with the saline extract (C1), but was strongly positive in the other lutjanid preparations (C, 2–4).

The purification procedure for the 66 kDa protein was repeated 4 times, with an average yield of 119 µg/g of the whole *L. griseus* saline extract. The protein was determined to be a single-chain polypeptide under reducing conditions in SDS-PAGE. The trace glycoprotein was not albumin (Hartmann et al, 1994), and under nonreducing, nondenaturing conditions, the lutjanid glycoprotein migration differed from human or bovine albumin (mol. weight 66 kDa, data not shown).

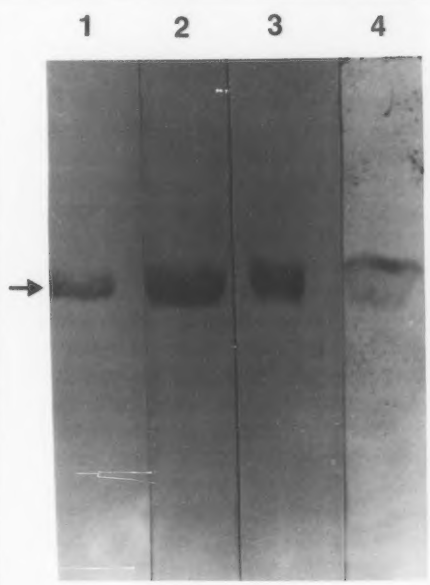

Figure 2

Western blot analysis of *L. griseus* life cycle stages. Samples included are purified 66 kDa protein, 1 µg total protein (lane 1); 50% ammonium sulfate supernatant fluid from a saline extract of female oocytes, 330 µg total protein (lane 2); saline extract of juvenile fish, 118 µg total protein (lane 3); saline extract of a sexually mature fish, 340 µg total protein (lane 4). The blot was developed with goat anti-*L. griseus* 66 kDa protein IgG as the primary antibody and with horseradish peroxidase-conjugated rabbit anti-goat IgG as the secondary antibody. The arrow marks the position of the 66 kDa protein.

After purification of the 66 kDa protein and production of a specific goat antiserum, saline extracts of different life stages of *L. griseus* were tested for the presence of the protein. Western blot analysis (Fig. 2) showed that the protein was present in all stages: oocyte (lane 2), juvenile (lane 3), and adult (lane 4).

Saline extracts of 14 species of adult lujanids and the hybrid (*L. synagris* × *O. chrysurus)* were prepared by the same method (see Materials and Methods section), and each extract was adjusted to 235 µg total protein. After Western blot analyses of the 15 different specimens, each blot was evaluated for the 66 kDa protein by visual inspection as shown in Figure 3, and the species were classified, as shown in Table 2. The species judged strongly positive were *L. griseus, L. jocu,* and *L. apodus* because for these three species the staining intensity of band patterns was approximately equal. Weak reactors were *L. buccanella, O. chrysurus, P. aquilonavis, L. synagris, L. analis, A. dentatus,* and *L. campechanus; L. vivanus, L. mahogoni, L. cyanopterus, E. oculatus,* and the hybrid exhibited no reaction.

Because the staining patterns of the 66 kDa proteins of *L. griseus, L. jocu,* and *L. apodus* were of similar intensity and because seven other species reacted weakly with the anti-66 kDa IgG for Western blots (Table 2; Fig. 3), an important question was raised: Was the protein from the different species identical but present in diminished concentrations, or were dissimilar determinants being detected? To investigate these questions, we selected *L. griseus, L. jocu,* and *L. apodus* because their 66 kDa proteins were strongly reactive with the specific antiserum. In addition, other studies have shown close phylogenetic relationships among these three species through morphological and biochemical data (Rivas, 1966; Vergara, 1980; Chow and Walsh, 1992) and by analysis of mitochondrial DNA sequences (Chow et al., 1993; Sarver et al., in press). Figure 4 shows the results of adsorbing the goat anti-66 kDa IgG with gluteraldehyde-insolubilized *L. apodus* saline extract for 24 h at 4°C. Comparing the Western blot in A (preadsorption) with B (postadsorption), we found that the antiserum reacted equally well with the *L. griseus* marker protein (lane 1, A and B) and the *L. griseus* saline extract (lane 4, A and B). The preadsorption antiserum also reacted with equal potency with *L. jocu* (lane 2A) and *L. apodus* (lane 3A). After adsorption of the antiserum with the insolubilized *L. apodus* saline extract, bands in the Western blots for *L. jocu* (lane 2B) and *L. apodus* (lane 3B) were

greatly reduced in reactivity with the secondary rabbit anti-goat IgG antiserum. The same anti-66 kDa IgG was adsorbed two more times with fresh, insolubilized *L. apodus* saline extract for 24 h at 4°C, and Western blots showed that the reaction of *L. jocu* was completely eliminated, whereas a trace reaction by *L. apodus* was detectable. The marker protein and the *L. griseus* extract reactions were similar to those in Figure 4 (data not shown). Therefore, we conclude that the 66 kDa protein from *L. griseus* must have different and multiple immunodominant regions compared with the 66 kDa proteins of *L. jocu* or *L. apodus*. Otherwise, after the third adsorption of the antiserum with insolubilized *L. apodus*, the immunoblots in B1 and B4 would have been greatly reduced or negative with the extract of *L. griseus*, but they were similar to the preadsorption blots.

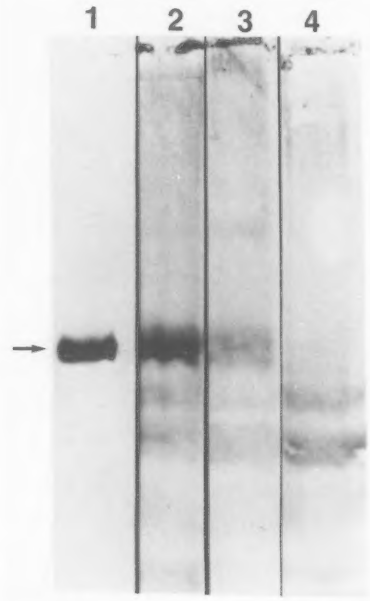

Figure 3

Western blot analysis of the graduated reaction of lutjanid saline extracts to anti-66 kDa protein IgG (primary antibody) followed by horseradish peroxidase rabbit anti-goat IgG (secondary antibody). The samples are as follows: lane 1 = purified *L. griseus* 66 kDa protein, 0.34 µg total protein; lane 2 = *L. griseus* extract, 235 µg total protein, classified as a strong reaction; lane 3 = *O. chrysurus* extract, 235 µg total protein, classified as a weak reaction; and lane 4 = *L. cyanopterus* extract, 235 µg total protein, classified as not detected. The arrow marks the position of the 66 kDa protein. Table 2 shows the reactions of soluble saline extracts of 14 different lutjanid species with the goat anti-*L. griseus* 66 kDa protein IgG.

The 66 kDa protein was purified separately from soluble extracts of the three species as described in Table 1. Figure 5 shows the proteins after SDS-PAGE and Western blots. The only discernible difference was that the 66 kDa protein from *L. griseus* migrated slightly slower than the proteins from *L. jocu* and *L. apodus*, indicating a slightly heavier molecular mass.

Next, it was determined that all three proteins are glycosylated when the method of O'Shannessy et al. (1987) is used. Separately, each of the purified proteins was oxidized with Na periodate. Available carbohydrate moieties were then labeled with biotin-hydrazide. After SDS-PAGE, glycoproteins were detected with peroxidase-labeled streptavidin and 4-chloro-l-naphthol (data not shown).

Finally, N-terminal amino acid sequences of the three proteins were obtained for comparative studies. Table 3 shows that the sequences from *L. griseus* and *L. jocu* for the first ten amino acids were approximately the same (residue no. 4 was not interpretable for *L. griseus*). Comparison of *L. griseus* with *L. apodus* showed that only as many as 3 of 10 amino acids were the same. In addition, only 3 of 10 amino acids of *L. jocu* were the same as *L. apodus*. Thus, as

Table 2

Screening of soluble saline extracts of fourteen different species and one hybrid of family *Lutjanidae* for presence of 66 kDa *L. griseus* protein by Western blot analyses. The basis for the strongly positive, weak, and not detected evaluation is shown in Figure 3. Each individual species was adjusted to 235 µg total protein for the immunoblots.

Species	Western blots for 66 kDa protein
L. griseus	
L. jocu	Strongly positive
L. apodus	
L. buccanella	
O. chrysurus	
P. aquilonaris	
L. synagris	Weak
L. analis	
A. dentatus	
L. campechanus	
L. vivanus	
L. mahogoni	
L. cyanopterus	Not detected
E. oculatus	
O. chrysurus × *(hybrid)*	
L. synagris	

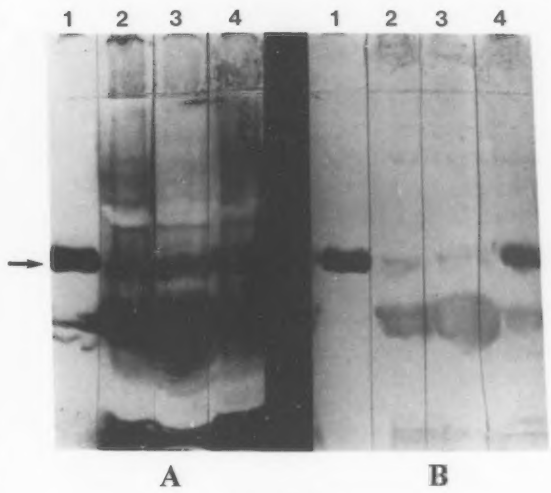

Figure 4

Western blot analysis of saline extracts from three closely related lutjanids, *L. griseus, L. jocu,* and *L. apodus.* The goat anti-*L. griseus* 66 kDa protein IgG was used before (**A**) and after (**B**) adsorption with 100 mg of insolubilized *L. apodus* saline extract for 24 h at 4°C. Lane 1 = purified *L. griseus* 66 kDa marker protein, 1 µg total protein; lane 2 = *L. jocu* extract, 235 µg total protein; lane 3 = *L. apodus* extract, 235 µg total protein; and lane 4 = *L. griseus* extract, 235 µg total protein. The arrow marks the position of the 66 kDa protein.

far as the first ten N-terminal amino acids, the 66 kDa protein of *L. apodus* was different from that of *L. griseus* and *L. jocu.*

Because other studies have shown *L. griseus, L. apodus,* and *L. jocu* to have a close phylogenetic relationship (e.g. Sarver et al., in press), we wanted to determine if there were obvious differences in their respective protein profiles. Fifty percent of A.S. precipitates of saline soluble extracts of each species were prepared at the same time; the precipitates were solubilized and dialyzed with saline, and they were compared in SDS-PAGE. Figure 6 shows that the 66 kDa protein was present in each of the three species (open arrow). However, there are at least three proteins that were present in *L. apodus* that were not detectable in *L. griseus* (closed arrows). Although other lutjanids have not been screened for these proteins, this procedure increases the possibility of isolating species specific proteins for antibody production, and eventually for species identification of early life history forms. Even if one or more of the three proteins of *L. apodus* were present in other lutjanids, some of the determinants on each protein, including different amino acid or glycan substitutions, or both, would probably be structurally different and thus would increase the possibility of producing specific monoclonal antibodies.

Discussion

A trace single-chain 66 kDa glycoprotein was purified to homogeneity by FPLC technology, starting with soluble extracts of adult *L. griseus* (Table 1; Fig. 1). The glycoprotein was not detected in Western blots with the biotinylated goat anti-whole *L. griseus* antiserum, but it was identified in extracts on SDS-PAGE (Fig. 1). This finding is not unusual because trace proteins in human serum frequently are not reactive with an antiserum produced in animals to whole human serum (senior author's unpubl. observations). A polyclonal antiserum was produced to the purified glycoprotein in a goat, and after removal of nonspecific reactivity by adsorption with insolubilized snapper and nonsnapper proteins, Western blots were carried out with the IgG fraction of the antiserum and with soluble extracts of 14 other lutjanid species that were available to us. Because of a comparatively strong reaction in Western blots

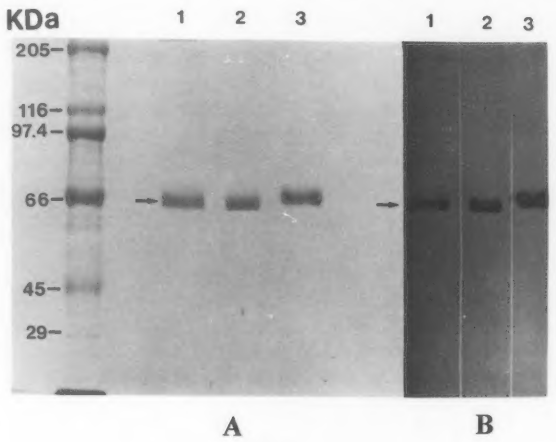

Figure 5

SDS-PAGE (**A**) and corresponding Western blots (**B**) of the highly purified 66 kDa proteins from 1) *L. jocu*, 2) *L. apodus*, and 3) *L. griseus*. Total protein added to each lane was 2 µg. The protein of *L. griseus* is slightly heavier compared with the other two species. Comparative N-terminal amino acid sequences of the three proteins are shown in Table 3.

Table 3

The N-terminal amino acid sequence analysis of the 66 kDa glycoproteins purified from *L. griseus*, *L. jocu*, and *L. apodus*.[1]

Snappers	1	2	3	4	5	6	7	8	9	10
L. griseus	Asp/Ala	Glu	Ala	N.I.[2]	Ala	Asp	Ala	Glu	Glu	Val
L. jocu	Asp	Glu	(Ala)[3]	His	Ala	Asp	Ala	Glu	Glu	Val
L. apodus	Asp	Glu/Ala	His	Ala	Asp	Ala	Glu	Glu	Val	Pro

[1] Analyzed at the University of Florida, Dep. of Biochemistry and Molecular Biology (ICBR Protein Chemistry Core Facility), Gainesville, FL.
[2] Not interpretable.
[3] Confidence: ( ) = possible/low.

with the antiserum, we purified to homogeneity similar 66 kDa glycoproteins from *L. jocu* and *L. apodus* (Fig. 5). The antiserum reacted weakly in immunoblots with soluble extracts of seven other species of lutjanid and did not react with extracts of four more lutjanid species and a hybrid of *O. chrysurus* and *L. synagris* (Table 2). The results indicated that the protein had both interspecies and species-specific determinants. In additional experiments, adsorption of the IgG fraction of the anti-66 kDa antiserum with glutaraldehyde-insolubilized *L. apodus* extract resulted in an antiserum that remained strongly reactive with *L. griseus* extracts but that was weakly reactive with *L. apodus*, and negative with *L. jocu* in Western blots (Fig. 4). Although the N-terminal amino acid sequence analyses of the first ten residues of *L. griseus* and *L. jocu* were approximately the same, only three of the ten residues were the same from *L. apodus*. These analyses did not take into account the possibility that the interspecies 66 kDa proteins may have different carbohydrate moieties that influence the antigenicity of the respective epitopes. For example, the 66 kDa protein of *L. griseus* was slightly heavier compared with the proteins of *L. jocu* and *L. apodus* in SDS-PAGE (Fig. 5) and thus could account for, but not prove, differences in glycan-dependent epitopes.

This approach was used as a model for distinguishing the different species of lutjanids. The eventual goal of these studies is to produce species-specific

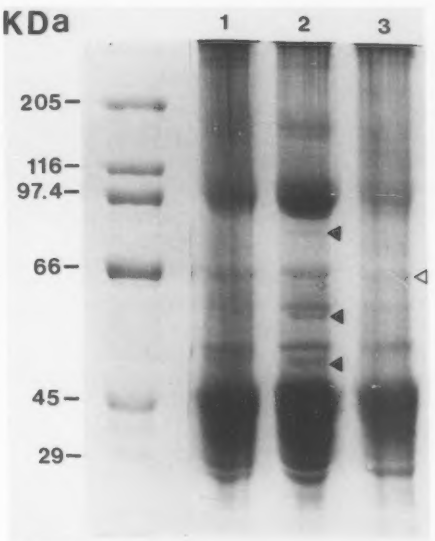

Figure 6

SDS-PAGE of the dissolved precipitates from the ammonium sulfate fractionation (0.38 mg/mL) of soluble extracts of 1) *L. jocu*; 2) *L. apodus*; and 3) *L. griseus*. Total protein added to each lane was 235 µg. The open triangle (◁) shows the position of the 66 kDa protein; the closed triangle (◀) marks bands not seen in *L. griseus* (lane 3). The gel was stained with Coomassie brilliant blue.

polyclonal and monoclonal antisera for identifying specimens at an early life stage. Animals will be immunized with highly purified proteins to enhance possibilities of producing antibodies to minor structural protein differences. The use of highly purified protein is especially important for monoclonal antibody production because immunization with complex mixtures of antigens generally results in monoclonal antibodies being produced to immunodominant epitopes (Barclay and Smith, 1986; Matthew and Sandrock, 1987). Immunization with a highly purified protein increases possibilities of producing monoclonal antibodies with a fine degree of specificity for each species of lutjanid. It remains for future experiments to determine if these specific antisera will also be species specific for life history specimens, such as eggs, larvae, and early juveniles. Although the anti-66 kDa IgG used in these studies also reacted with the early life history specimens of *L. griseus* (Fig. 2), future experiments with monoclonal antibodies generated to the 66 kDa protein and other lutjanid proteins (Fig. 6) will determine their usefulness as specific reagents.

In other studies, the use of a very pure antigen was successful for predator-prey studies with *Sciaenops ocellatus* (red drum) (Schultz and Clarke, 1995; Arnold et al., in press), in which a specific polyclonal antiserum was prepared by immunizing a goat with a highly purified 80 kDa glycoprotein.

Monoclonal antibodies were used successfully to detect epitopes in a number of marine and fresh water species. For example, An et al. (1990) used a low molecular weight eluate from SDS-PAGE slab gels of a protein extract from rock shrimp to produce highly specific murine monoclonal antibodies. A monoclonal antibody to partially purified mature egg proteins reacted with eggs, embryos and larvae of *Asterina pectinifera* but not with other species belonging to the same genus or in mixtures of biological specimens of marine origin (Ikegami et al., 1991). Murine monoclonal antibodies were employed by Miller et al. (1991) to distinguish three barnacle species of similar size, and Beck et al. (1992) investigated surface antigens of rainbow trout sperm with monoclonal antibodies.

Immunological detection methods with monoclonal antibodies have also been valuable for many aspects of seafood science. Recently, Huang et al. (1995) were able to distinguish the commercially valued red snapper, *L. campechanus*, from less valuable substitutes by using ELISA with two monoclonal antibodies raised to a red snapper protein.

It is now evident that identification of species of the western Atlantic snapper at early life history stages by examining external features alone is insufficient and that new methods are necessary to increase our knowledge. The use of highly purified lutjanid proteins, together with the production of polyclonal and monoclonal antibodies for a variety of immunoassays, has wide versatility and applicability for future studies.

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Forecasting the fishery for pink shrimp, *Penaeus duorarum*, on the Tortugas Grounds, Florida

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Abstract.—In this report I review the biology of and fishery for pink shrimp, *Penaeus duorarum*, harvested from the Tortugas Grounds off southwest Florida, and present models used to forecast annual pink shrimp landings in this area. Pink shrimp spawn all year, and larvae recruit to nurseries in the seagrass-mangrove ecosystem surrounding Everglades National Park and Florida Bay. Juveniles move out of the nurseries all year, but catch per unit of effort for smallest size classes generally exhibits March and September peaks. Total landings usually rise sharply in November and taper off after April. The fishery was relatively stable during 1960–85, averaging 4,350 metric tons annually, but it has shown a singular decline and potential recovery since 1985. In 1987, I began forecasting annual landings by using multiple regression analyses of fishery catch statistics and environmental factors that could affect survival, growth, and recruitment. Potential predictor variables from May through October were investigated in order to release a timely annual forecast by November. Each year, the updated data set from 1966 onwards was examined to derive the "best" forecast models. Important predictor variables included indices of fishing activity during the waning months of the fishery (May–July) and surface and ground water levels within Everglades National Park during June-September. Forecasts were within ±20% of actual landings for five of eight years, whereas forecast direction (increase or decrease over the prior year) was usually correct. Cause-effect relationships between predictor variables and pink shrimp recruitment to the fishery remain to be determined.

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Fishery Bulletin 94:743–755 (1996).

The pink shrimp, *Penaeus duorarum*, fishery over the Tortugas Grounds, southwest of Florida, averaged 4,525 metric tons (t) of shrimp tails per year during 1960–80 (Nance and Patella, 1989). Landings began to decline in the mid-1980's, collapsed to 2,000 t during 1988–91 for no apparent reason, and rebounded to over 4,000 t in 1994.[1,2] Coincident with this unprecedented decline, the Gulf of Mexico Fishery Management Council (GMFMC) requested that the National Marine Fisheries Service (NMFS) evaluate the possibility of forecasting annual landings for the Tortugas pink shrimp fishery. The Gulf of Mexico Fishery Management Council and NMFS expected that such a model could aid in the planning and evaluation of management actions and could assist shrimp fishermen in preparing for the upcoming fishing season. NMFS has been forecasting annual brown shrimp, *P. aztecus*, landings for Texas since 1962 (Berry and Baxter, 1969; Baxter and Sullivan, 1986) and for Louisiana since 1985.[2] Annual forecasts are released to the fishing industry in newsletters and direct mailings. Forecasting models for the Tortugas pink shrimp fishery have been proposed previously (Yokel et al., 1969; Browder, 1985). However, Yokel et al. never implemented their model, and Browder's annual models provided relatively poor forecasts for the three years beyond her base data set (estimated from Fig. 9 in Browder [1985] to be –24%, +53%, and +56% of actual 1981, 1982, and 1983 landings, respectively).

In this report I review both the biology of and the fishery for pink shrimp in southern Florida. I then present empirical models used by NMFS since 1987 to forecast annual Tortugas pink shrimp landings. These models are based on environmental conditions in the primary pink shrimp nurseries of Florida Bay, Everglades National Park, and adjoining coastal waters. Pink shrimp production is likely linked to survival and growth of juveniles in these habitats. For example, high water levels in Everglades National Park during October–December and January–March were associated with subsequent high pink shrimp catches in January–March and April–June, respectively (Browder, 1985). A disruption in nursery habitat functions, such as those resulting from seagrass mortality (Robblee et al., 1991) or freshwater diversion (Light and Dineen, 1994), may have been causes of previously noted fluctuations in pink shrimp harvest.

[1] Nance, J. M. 1994. A biological review of the Tortugas pink shrimp fishery through December 1993. Unpublished report to the Gulf of Mexico Fishery Management Council, National Marine Fisheries Service, 4700 Avenue U, Galveston, TX 77551, 11 p.

[2] National Marine Fisheries Service. 1985–1994. 4700 Avenue U, Galveston, TX 77551. Unpubl. data.

The predictive model(s) was intended to provide an estimate of a future 12-month total pink shrimp catch with a forecast issued in advance of the main shrimping season. For the Tortugas fishery, monthly catches generally rise sharply in November and taper off after April (Nance and Patella, 1989). Ideally, the forecast should be released to the industry no later than October. In practice, however, there are time delays between data collection for a given month and availability of final data. My goal was to release a forecast by October $_{Yr.t}$ for the November $_{Yr.t}$ through October $_{Yr.t+1}$ "fishing year."

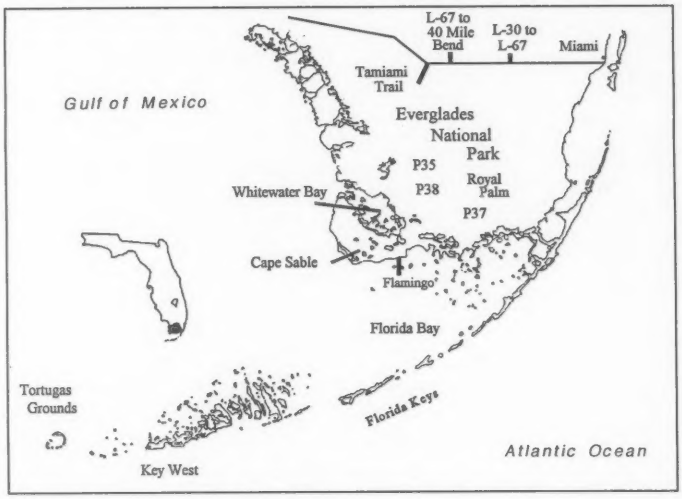

Figure 1

Location of the Tortugas pink shrimp grounds in relation to the southern Florida environmental data sources. P35, P37, and P38 are wells in Everglades National Park. Rain gauges are located at Flamingo, Royal Palm, and Tamiami Trail. Surface water discharge gates are located at L-67 to 40-Mile Bend and at L-30 to L-67.

Since the fishery's inception in 1949, researchers have postulated that landings from the Tortugas Grounds were dependent on survival and growth of postlarval and juvenile pink shrimp in primary nursery habitats of Florida Bay and Whitewater Bay (Fig. 1). Female shrimp in spawning condition were found all year on the Tortugas Grounds west of Key West, with the highest frequency of ripe females occurring April through July (Ingle et al., 1959; Cummings, 1961). Larval stages were found all year in waters west and south of Florida Bay but were generally most abundant in the same months as ripe females (Munro et al., 1968; Jones et al., 1970). Postlarval stages also were found all year, but late postlarval stages were found primarily near the coast and in Florida Bay and Whitewater Bay (Tabb et al., 1962; Jones et al., 1970; Roessler and Rehrer, 1971; Allen et al., 1980). Larval and postlarval stages were first thought to migrate into Florida Bay by riding surface waters on the eastward tidal excursion and by dropping to the bottom either during westward tidal movement (Koczy et al., 1960) or after detecting lower salinities (Hughes, 1969). Alternatively, currents were hypothesized to sweep larvae south and east of the spawning grounds and along the south side of the Florida Keys until larvae entered Florida Bay through passes between the keys (Rehrer et al., 1967; Munro et al., 1968). Recent research on larval shrimp distributions in relation to currents has indicated that both immigration methods may be effective (Criales and Lee, 1995).

Postlarvae reaching coastal seagrass and mangrove nurseries encounter several distinctive environments: Florida Bay seagrass beds are frequently hypersaline, the Whitewater Bay ecosystem is estuarine, and the Florida Keys are oceanic (Tabb et al., 1962; McIvor et al., 1994). Catches of postlarval and juvenile pink shrimp were highest in seagrasses of western Florida Bay and the middle Florida Keys, moderate in central Florida Bay and the lower Keys, and low to absent in eastern Florida Bay (Costello et al., 1986; Holmquist et al., 1989). Pink shrimp also recruit to the mangrove-lined Whitewater Bay system and were found to be more abundant in submerged aquatic vegetation than in nonvegetated areas during trawl surveys (Idyll and Yokel, 1970). Higher densities of pink shrimp are associated with seagrass (*Thalassia testudinum* and *Halodule wrightii*) habitats than with algal, red mangrove (*Rhizophora mangle*) prop root, or nonvegetated habitats (Sheridan, 1992; Sheridan et al.[3]). Widespread mortality of seagrasses (Robblee et al., 1991) thus might be expected to reduce subsequent pink shrimp harvests.

Juvenile pink shrimp exhibit early spring and late summer peaks in abundance in western Florida Bay (although only a single summer peak has been observed for the last decade[4]) and move out of coastal habitats on ebb tides, at night, during full and new moons (Tabb et al., 1962; Hughes, 1968; Yokel et al.,

[3] Sheridan, P., G. McMahan, G. Conley, A. Williams, and G. Thayer. 1996. Response of macrofaunal communities to seagrass mortality in Florida Bay (Florida, USA). I. Shallow bank-top habitats. In review.

[4] Robblee, M. 1995. National Biological Service, Southeastern Research Program, Florida International University, Miami, Fl 33199. Unpubl. data.

1969). Rapid salinity changes, as might be experienced during rainy season floods, may also force shrimp out of nearshore habitats (Hughes, 1969). Emigration of juvenile pink shrimp from nurseries in summer and fall has been postulated to form the fall and winter landings of new recruits by the fishery (Higman et al., 1972). Juvenile and subadult pink shrimp marked and released in southwest Florida coastal habitats were primarily recaptured on the Tortugas fishing grounds (Costello and Allen, 1966; Gitschlag, 1986). Apparent pink shrimp movement speeds were 1–2 km/day (Costello and Allen, 1966); thus pink shrimp could reach the fishing grounds 100 km southwest of Cape Sable (Fig. 1) in 50–100 days, as postulated by Higman et al. (1972).

Environmental determinants of pink shrimp growth and survival have not been examined extensively. Most available information consists of pink shrimp abundance and size by season or habitat, with coincident measurements of temperature and salinity. Pink shrimp have wide tolerances for salinity and temperature (0–65‰ and 11–40°C; Costello and Allen, 1970; Costello et al., 1986). Maximum growth of postlarval pink shrimp (7.8–10.1 mm total length [TL]) was found at 30–35°C under constant salinity (28–32‰, Teinsongrusmee, 1965). The only experimental analyses of pink shrimp survival versus combined temperature and salinity variations was conducted by Williams (1960). Survival of juveniles (35–100 mm TL) was highest (77–100%) at 15–30‰ and 8.8–28.4°C but was significantly lower (62–67%) at 10‰ and 8.8–28.4°C due to impaired osmoregulation. Higman et al. (1972) conducted enclosure experiments to determine pink shrimp growth in the field but felt that poor water quality conditions confounded their results. Neither Williams (1960) nor Teinsongrusmee (1965) addressed the hypersaline conditions often experienced in Florida Bay (up to 70‰; McIvor et al., 1994).

The Tortugas fishery began in 1949, and since 1956 monthly catch and effort data have been collected by NMFS personnel using standard methods (Nance and Patella, 1989). The fishery has landed an average of 4,350 metric tons (t) annually during 1960–85 (NMFS[2]) and was relatively stable (coefficient of variation=17%; Nance and Patella, 1989). Since that time, however, the fishery has shown a singular, and as yet unexplained, decline and apparent recovery (Fig. 2). In conjunction, the bimodal trend in monthly catch per unit of effort (CPUE) of the smallest pink shrimp size class (≥68 tails to the pound, or "68-count") has changed (Fig. 3). The fall peak in recruitment of 68-count pink shrimp that dominated in early years (1960–69) has shifted in favor of a spring peak. This shift may have been the result of management measures enacted during 1961–81 to restrict the catch of small shrimp (Caillouet and Koi, 1981; Gulf of Mexico Fishery Management Council, 1981).

Materials and methods

Fishery yield forecasts often depend upon indices of larval or juvenile abundance as indicators of recruitment into a fishery. Forecasting brown shrimp yield off Texas depends upon landings of juveniles by the Galveston Bay bait shrimp industry immediately prior to their emigration from the bay (Berry and Baxter, 1969; Baxter and Sullivan, 1986). Forecasting western rock lobster, *Panulirus cygnus*, yield is based on seasonal settlement of the final planktonic stage (puerulus) on collectors at a single site, Seven Mile Beach, Western Australia (Phillips, 1986). In Florida, however, there are no long-term fishery-independent data sets describing larval or juvenile pink shrimp abundance in coastal habitats. Thus, my models are based on fishery-dependent catch statistics and on environmental variables that could affect the survival, growth, and recruitment of pink shrimp, even though causal mechanisms may be

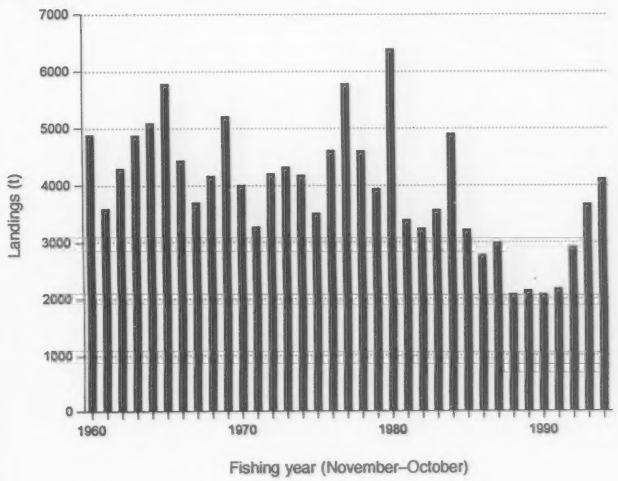

Figure 2

Annual landings by the Tortugas pink shrimp fishery (NMFS, Footnote 2 in the text).

unknown. The above review of the literature indicated that factors affecting larval and juvenile pink shrimp abundance and survival during the months of May–October were most likely to affect recruitment to the next fishing year.

Data sources

Development of forecasting models requires sets of long-term data collected in a consistent manner. There are no long-term environmental or biological data sets from within Florida Bay per se (Schmidt and Davis, 1978), with the exception of an historical salinity data set that has been compiled by the National Biological Service.[4] Thus, the primary sources of long-term data used in my models were those with physical or biological factors for May–October in locations near Florida Bay. These sources were the U.S. Department of Commerce (National Weather Service [NWS]; National Ocean Service [NOS]; and NMFS) and the U.S. Department of the Interior (Everglades National Park [ENP]).

National Weather Service stations in Key West and Miami, Florida, bracket Florida Bay and Everglades National Park (Fig. 1). The NWS collects data that provide hourly, daily, and monthly maxima, minima, means, and totals for climatic factors.[5] Monthly values at each site were compiled for the following variables: mean air temperature; total heating and cooling degree days (on any given date, one degree day accrues for each °F that the mean temperature falls below or above 65°F [18.3°C], respectively); total days with air temperatures ≤55°F (13°C) and ≥90°F (32°C) to examine effects of temperature extremes; mean wind speed; mean cloud cover; and total rainfall.

NOS records monthly sea level data at Miami Beach and Key West, Florida. I compiled monthly mean sea level data for Key West (station number 8724580), the tide gauge used by NOS to develop tide tables for Florida Bay.[6]

ENP maintains a series of ground water wells, surface water discharge gates, and rain gauges to monitor hydrology within the park.[7] I compiled the following data: mean monthly water level at three wells closest to the coast (P35 and P38 in Shark River Slough flowing into Whitewater Bay and the Gulf of Mexico, and P37 in Taylor Slough flowing into central Florida Bay); monthly total surface water discharge into northern ENP via two sets of water control structures (Canal L-67 to 40-Mile Bend and Canal L-30 to Canal L-67, later referred to as L-67 and L-30) along the Tamiami Trail, U.S. Highway 41; and total monthly rainfall at three gauges within the park (from south to north: Flamingo, Royal Palm, and Tamiami Trail; Fig. 1). In 1987, a correlation analysis of the ENP, Key West, and Miami monthly rain data was conducted for the period 1963–86. Although all five gauges were significantly correlated (r=0.514–0.792, P<0.05), the Royal Palm gauge had the highest correlations with gauges other than Key West (r=0.773–0.792). Lowest correlations were found between Key West and other gauges (r=0.514–0.609). For these reasons, Royal Palm was selected as the primary rainfall indicator (Miami was substituted directly in 1993 because of disruptions in ENP data availability caused by Hurricane Andrew).

Finally, NMFS collects monthly catch and effort data (and thus catch per unit of effort, CPUE) by various size classes for shrimp fisheries in the Gulf of Mexico.[8]

[5] National Weather Service. 1963–1994. Local climatological data, monthly summaries for Miami and Key West, Florida. NOAA, National Climatic Data Center, Asheville, NC 28801.

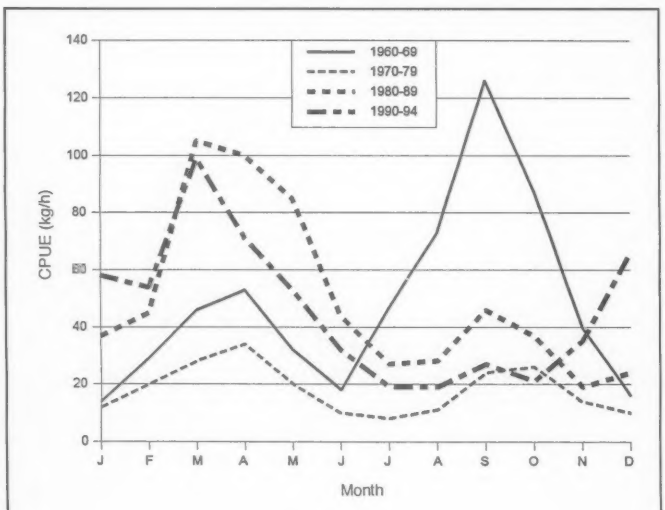

Figure 3

Decadal average monthly catch per unit of effort (CPUE) of 68-count pink shrimp (NMFS, Footnote 2 in the text).

[6] National Ocean Service. 1963–1994. Tides, high and low waters. NOAA, National Ocean Service, Tidal Analysis Branch, Silver Spring, MD 20910.

[7] Sikkema, D., and G. Schardt. 1987–1994. Hydrological Section, South Florida Research Center, Everglades National Park, Homestead, FL 33034. Unpubl. data.

[8] National Marine Fisheries Service, Statistics Operation Team. 1960–1994. 75 Virginia Beach Drive, Miami, FL 33149. Unpubl. data.

I compiled monthly pink shrimp catch, effort, and CPUE for all sizes combined and for the smallest size category (≥68 tails to the pound or "68-count") in NMFS statistical subareas 1–3 off southwestern Florida.

In addition to monthly values for these 29 variables, two quarterly means or totals for each variable (May–July and August–October) were created. These data resulted in a suite of 232 variables (29 variables × 6 months plus 29 variables × 2 quarters) as potential predictors. All data were received and analyzed in American system units (e.g. shrimp in pounds, rainfall in inches). Actual and predicted landings are presented in metric equivalents. Analyses began with the year 1966 because it was the approximate completion date for the system of major water control structures that influence ENP and Florida Bay (Light and Dineen, 1994).

Statistical analyses

The statistical relationships of annual pink shrimp catches in NMFS statistical subareas 1–3 with environmental and biological variables were examined by multiple linear regression. The tentatively entertained models were of the form

$$C = b_0 + b_1x_1 + b_2x_2 + \ldots b_kx_k,$$

where C = total November$_{Yr.\ t}$–October$_{Yr.\ t+1}$ pink shrimp catch;
x_k = variables measured during May–October;
b_k = regression coefficients; and
k = number of variables in the model.

For the first forecast (released in November 1987), environmental and biological data for May–October 1966–86 were used to develop descriptive ("hindcast") models, whereas data for May–October 1987 were reserved for the forecast. Initial regression analyses employed the "R-square" option of the SAS regression procedure (SAS Institute Inc., 1985) to capitalize on the power of Mallow's test statistic C_p. This option produces regression equations and multiple R^2 values for all possible subsets of p variables, allowing the investigator to choose the "best" linear model(s) based on R^2. Mallow's C_p statistic detects a "best" set of explanatory variables that minimizes both error due to too few variables and variance of predictions due to too many variables (Daniel et al., 1971). Regression equations with $C_p > p$, where p = number of variables in the equation, have increased bias whereas equations with $C_p < p$ have increased error. Regression equations including more than one form of a variable, such as those with a quarterly variable plus one or more of its component months, were not allowed. For models with $C_p \approx p$, stepwise regression (F-to-enter=0.25 and F-to-stay=0.25) was used to determine all partial and full statistics. The Durbin-Watson statistic was used to assure that autocorrelation in the selected models was minimal (i.e. that errors in regression were independent; Draper and Smith, 1981). The relationship between residuals and fitted values was examined to assure constant variance. Residuals were checked against Cook's statistic to assure that outliers did not unduly influence model coefficients (Draper and Smith, 1981). Models passing all these tests were employed for the annual forecast. Model performance was assessed by examining the direction of the forecast (whether landings increased or decreased over the prior year) and the accuracy of the forecast (expressed as percent above or below actual landings). Forecasts in the same direction and with accuracies of actual landings ±20% were termed successful.

After 1987, data sets were updated regularly and the regression procedures were repeated each year for the annual forecast, beginning with development of new descriptive models.

Results

Of the 232 possible predictors, only 30 monthly variables and two quarterly variables have ever appeared in the 26 forecast models generated since 1987 (Table 1). Only a few of these variables have occurred on a regular basis, including in decreasing frequency: 1) days fished during July; 2) ENP L–67 discharge during September and June; 3) ENP groundwater level in wells P38 during August and P37 during September; 4) CPUE of 68-count pink shrimp during May, and 5) Key West wind speed in September. Relationships of these variables to subsequent fishing year landings are illustrated in Figures 4–7. Five- and six-variable models incorporating four or more of these variables provided the most accurate forecasts.

Single forecast models were used in 1987 and 1988, whereas all other forecasts employed 2–4 models (Table 2). In multiple-model years, models usually differed by a single variable, and tests for selecting those models (Mallow's C_p and R^2) gave little reason for favoring one model over another. One exception occurred in 1989 when two sets of models with different independent variables were developed (models 3 and 4 versus models 5 and 6 in Table 2). Forecasts released to the industry stated whether landings were expected to improve or decline and gave high and low landing estimates from the models. A set of revised models for 1993 (forecasts were not

Table 1

Variables included in at least one regression generated for 1987–95 Tortugas pink shrimp landings forecasts. Variables are monthly means or totals (month 5=May) except RRain57 and MRain57 which are summed over months 5–7. NMFS = National Marine Fisheries Service; ENP = Everglades National Park; NWS = National Weather Service; NOS = National Ocean Service. Data are received from sources in American system units (in parentheses). Abbreviations are used in Table 2. ac-ft = acre feet.

			Frequency of occurrence by month					
Source	Variable	Abbreviation	5	6	7	8	9	10
NMFS	Total pink shrimp catch (lb)	Pink		8				1
	Total fishing effort (days)	Days	1	1	20		2	
	Catch per unit of effort of 68-count pink shrimp (lb/day)	CPUE68	11	1		1	3	
ENP	Mean water level in well P35 (ft)	P35	1			3	4	
	Mean water level in well P37 (ft)	P37				1	9	
	Mean water level in well P38 (ft)	P38		1	1	15	1	5
	Total rainfall, Royal Palm (in)	RRain		1				
	Total rainfall during May–July, Royal Palm (in)	RRain57	3					
	Total surface water discharge, L-67 to 40-Mile Bend (ac-ft)	L67		14		2	19	2
NWS	Total rainfall during May–July, Miami (in)	MRain57	1					
	Mean air temperature, Key West (°F)	KAir						4
	Mean wind speed, Key West (mi/h)	KWind	3		2		9	
NOS	Mean sea level, Key West (ft)	Sea	1					

released to the industry) is included as well (Table 2) because Hurricane Andrew impacted south Florida in August 1992 and disrupted ENP data collection through the remainder of 1992 and into 1993. All data were held until ENP had verified that recording instruments had not been disturbed by the hurricane or that instruments had been resurveyed and appropriate corrections had been applied to data sets.[7] These revised forecasts are presented in Table 2 because ENP data figured prominently in every other model.

All models derived in 1987, 1990, 1991, 1992, and 1994 produced forecasts that were within ±20% of actual landings (Table 2). All 1990 and 1991 models (models 7–12) contained the same first five variables. Models 13 and 14 (1992) and models 22 and 23 (1994) contained similar independent variables as did successful 1990–91 models. Forecast models for 1989 included two relatively successful ones (models 3 and 4, –10% and +18% of actual landings) and two poor ones (models 5 and 6, +45% and +44% of actual landings). None of the 1989 models approached the Mallow's test criterion of $C_p = p$, but models 3 and 4 had relatively high R^2 values compared with those of models 5 and 6. Model 2 (1988) and models 15–17 (1993) produced unsuccessful forecasts. Model 2 was the only forecast equation that had no variable directly associated with the Tortugas fishery, although all other unsuccessful models did have such variables. Models 15–17 were derived without access to ENP data which had been incorporated in all other models, successful or otherwise. Had ENP data been available, models 18–21 would have been generated with all but model 19 producing successful forecasts. Models generally forecasted increases or decreases in future landings correctly, with exceptions in 1989, 1991, and 1993. In both 1989 and 1993, three of four models correctly forecasted increased landings, whereas in 1991 only one of three models correctly forecasted decreased landings. Finally, the forecast models for 1995 (for which actual landings will not be available until late 1996) are presented for comparison with previous models and as documentation of the wide range in forecasts (2,858–4,581 t) seen previously only in 1989.

Every model contained at least one independent variable measured in September, and some models included October measurements. These data were usually unavailable until November, thus my goal of releasing each forecast in October was never achieved.

The fact that several variables consistently entered forecast models that were generated annually argues for selecting a single model with fixed variables. This strategy was assessed by applying monthly data, collected in years after generating each model, to those models in order to determine accuracy, if a given

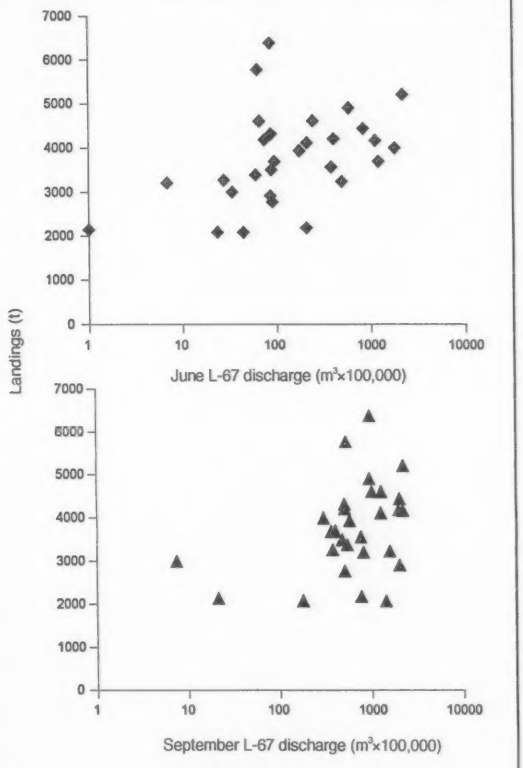

Figure 4

Scatterplots of surface water variables against subsequent fishing year landings, 1966–94.

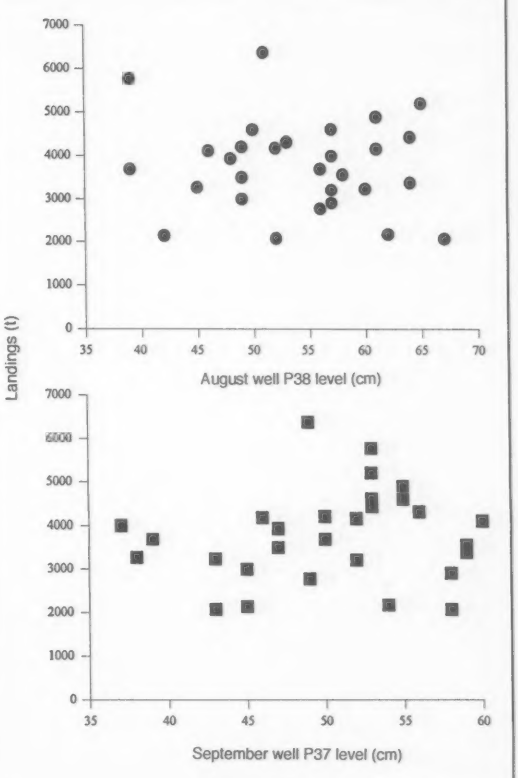

Figure 5

Scatterplots of well water levels against subsequent fishing year landings, 1966–94.

year's model had become "the" forecast model (Table 3). The results indicate that a model that successfully forecasts for the year it was developed does not always function well in succeeding years (e.g. models 1, 3, and 9) and that initially poor models can later become successful (e.g. models 5 and 6). Generating new forecast models each year from updated databases appears to be more accurate than using a fixed forecast model.

Discussion

These models were quite accurate at forecasting whether landings would increase or decrease and only moderately accurate at forecasting amounts landed, but they did not address cause-effect relationships between environmental variables and pink shrimp recruitment. The regular selection of only a few variables in the regression models, however, implies that determining the mechanisms behind selected variables describing Florida Bay and adjacent waters could provide the requisite data for more accurate forecasting of pink shrimp landings. Two classes of data regularly occurred as forecast variables: 1) measurements of upland freshwater supply during the rainy season, and 2) fishing activity on the Tortugas grounds during the waning months of a given fishing year.

Correlation between penaeid shrimp production and freshwater inputs have been recorded worldwide, even though the exact relationship between landings and freshwater may be site- or species-specific. In a previous study of the Tortugas pink shrimp fishery, quarterly landings were found to be either positively or negatively correlated with ENP ground water levels (Browder, 1985). Elsewhere, correlations between penaeid shrimp landings and rainfall, river discharge, or well-water levels have been positive (Hildebrand and Gunter, 1953; Gunter and Edwards,

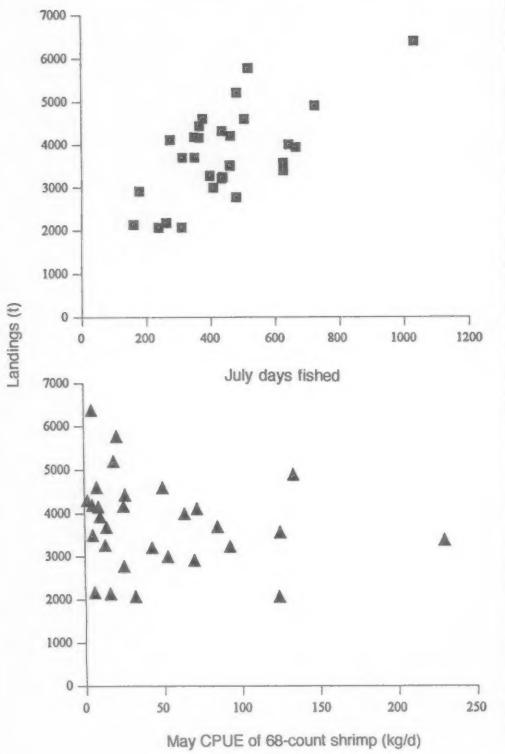

Figure 6

Scatterplots of fishery variables against subsequent fishing year landings, 1966–94.

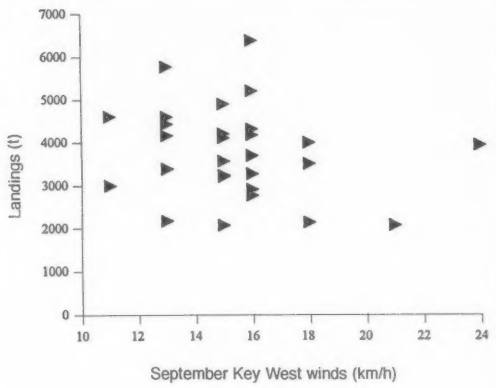

Figure 7

Scatterplot of September Key West winds against subsequent fishing year landings, 1966–94.

1969; Ruello, 1973; Edward, 1978; Glaister, 1978; annual model of Browder, 1985; Vance et al., 1985; Gracia, 1989), negative (Barrett and Gillespie, 1973, 1975; Barrett and Ralph, 1977), or absent (Glaister, 1978; Hettler and Chester, 1982).

In this analysis, freshwater indices exhibited both positive and negative influences on pink shrimp forecasts. Coefficients for L-67 surface water discharge into ENP were always positive, although the nature of the relationship is not as clear for September as it is for June (Fig. 4). The two years with highest landings (1980 and 1977) both occurred when there was moderate L-67 water discharge. Lowest pink shrimp production was associated with extremely low L-67 discharges during the drought of 1989–90. Coefficients for groundwater at well P37 (flowing toward Florida Bay) were always positive whereas those for well P38 (flowing toward Whitewater Bay) were always negative, but again the relationships to landings are not clear (Fig. 5). In most cases, including the present one, the mechanisms behind any relationship between freshwater and penaeid shrimp landings have not been determined experimentally. It has been postulated that excessive freshwater may prevent habitat utilization by postlarval penaeids (Barrett and Gillespie, 1973, 1975) or may initiate early movement of juvenile penaeids out of estuaries (Vance et al., 1985). Hypersalinity is a more frequent condition in Florida Bay (McIvor et al., 1994). Although the direct effects of hypersalinity on pink shrimp are unknown, low surface water discharges are associated with low landings. Examples of the linkage of freshwater inputs to other marine organisms include positive correlation with sea nettle, *Chrysaora quinquecirrha*, abundance in Chesapeake Bay (Cargo and King, 1990) and positive or negative correlation with production by several commercial fisheries in Maryland (Ulanowicz et al., 1982).

Another class of variables typically included in penaeid shrimp forecast models are indices of fishing activity or standing crop prior to the forecast period. The Texas brown shrimp forecast covers the July–June period and is based on average weekly CPUE by the Galveston Bay live bait shrimp fishery during April–June, just prior to emigration of the shrimp into the offshore fishery (Baxter and Sullivan, 1986). The Louisiana brown shrimp forecast also covers July–June, but it is based on inshore and offshore landings from the western half of the state during May.[2] Descriptive models for Tortugas pink shrimp (Browder, 1985) included indices for fishing effort and CPUE that were usually positive in nature and appeared to influence landings up to four

Table 2

Regression models and forecast versus actual Tortugas pink shrimp landings during fishing years 1987–95. See Table 1 for definitions of abbreviations of variables (V1–V6), listed with signs and in order of inclusion by stepwise regression. n = number of variables; Cp = Mallow's test; % = accuracy = 100 (forecast-actual)/actual.

		Variables in regression						Statistics			Landings (t)		
Year	Model	V1	V2	V3	V4	V5	V6	n	Cp	Mult. R^2	Forecast	Actual	%
1987	1	–KAir10	+P379	–CPUE688	+P386	+RRain6	—	5	5.20	0.849	3454	3000	15
1988	2	+RRain57	–L678	+P389	–P388	+L679	+P387	6	6.36	0.775	2857	2075	38
1989	3	–CPUE685	+Pink6	+L6710	+P379	+L676	—	5	6.53	0.883	1917	2141	–10
	4	–CPUE685	+Pink6	+L6710	+P379	+L676	–P3810	6	5.77	0.911	2516	2141	18
	5	+Days7	+RRain57	–P388	+L679	–KWind7	—	5	6.21	0.746	3100	2141	45
	6	+Days7	+RRain57	–P388	+L679	–KWind7	+P359	6	5.22	0.792	3081	2141	44
1990	7	+Days7	+L679	–P388	+L676	+P379	—	5	5.28	0.809	1904	2078	–8
	8	+Days7	+L679	–P388	+L676	+P379	+Pink6	6	6.31	0.819	1786	2078	–14
	9	+Days7	+L679	–P388	–P359	+P379	+L676	6	6.36	0.811	1911	2078	–8
1991	10	+Days7	+L679	–P388	+L676	+P379	—	5	5.16	0.810	2153	2179	–1
	11	+Days7	+L679	–P388	+L676	+P379	–P355	6	6.25	0.830	1993	2179	–9
	12	+Days7	+L679	–P388	+L676	+P379	–L678	6	6.02	0.822	2006	2179	–8
1992	13	+Pink6	–Cpue685	+P359	+Days9	–P3810	—	5	5.37	0.873	2830	2914	–3
	14	+Pink6	–Cpue685	+P359	+Days9	–P3810	+L679	6	6.02	0.897	3066	2914	5
1993	15	+Days7	–KAir10	–CPUE685	–KWind5	–CPUE689	+MRain57	6	6.16	0.880	1982	3696	–46
	16	+Days7	–KAir10	–CPUE685	–KWind5	–CPUE689	–Days6	6	6.01	0.861	1574	3696	–57
	17	+Days7	–KAir10	–CPUE685	–KWind5	–CPUE689	+Sea5	6	6.03	0.858	2106	3696	–43
1993	18	+Days7	+L679	–P388	–KWind9	+L676	+P378	6	6.20	0.898	3237	3696	–12
Revised	19	+Days7	+L679	–P388	–KWind9	+L676	–P3810	6	6.04	0.884	2531	3696	–32
	20	+Days7	+L679	–P388	+L676	–KWind9	+Days5	6	6.37	0.884	3738	3696	1
	21	+Days7	+L679	–P358	+L676	–KWind9	+Pink10	6	6.02	0.878	3483	3696	–6
1994	22	+Days7	+L679	–P388	–KWind9	+Pink6	–CPUE685	6	6.08	0.867	4517	4127	9
	23	+Days7	+L679	–CPUE685	+Pink6	–KWind9	–P3810	6	6.27	0.866	3709	4127	–10
1995	24	+Days7	–KWind9	–P358	+L676	+L679	–CPUE685	6	6.03	0.863	2858	—	—
	25	+Days7	–KWind9	–P358	+L676	+L679	–P388	6	6.00	0.861	3266	—	—
	26	+Days7	–KWind9	–P388	+Pink6	+L679	–CPUE685	6	6.16	0.861	4581	—	—

quarters (12 months) in advance of a given fishing year, thus covering new recruits and spawning stocks. In my models, fishing activity on the Tortugas Grounds during the waning months of a given fishing year (May–July) may be related to the status of the spawning stock and its future production of larvae during the summer and fall months. Catch and effort variables in these models had positive effects on forecasted landings, although CPUE variables had negative coefficients. These indices may be related to prerecruits or to potential parent spawning stocks, although there are no statistically significant parent stock-recruitment relationships for Gulf of Mexico *Penaeus* (Nance, 1993).

In a descriptive model for the North Carolina pink shrimp fishery (Hettler and Chester, 1982; Hettler, 1992), landings during February–July were positively correlated with water temperatures during the coldest two weeks of the preceding winter. Severe cold temperatures were postulated to have reduced landings by killing postlarvae and juveniles overwintering in estuaries (Hettler and Chester, 1982). The model successfully described landings within ±20% of actual landings in five of 10 years (Hettler, 1992). The opposite effect was seen in Florida (Browder, 1985), where mean January–March air temperature,

Table 3

Accuracy (% above or below actual landings) of Tortugas pink shrimp forecasts if forecast equations had become fixed in the year generated. Model = model number from Table 2. Boldface values are ±20% of actual landings.

		Accuracy (%)							
Year	Model	1987	1988	1989	1990	1991	1992	1993	1994
1987	1	**15**	153	55	72	109	87	**3**	**–17**
1988	2		38	56	56	58	119	**–1**	55
1989	3			**–10**	–29	39	–29	53	22
	4			**18**	**–13**	57	**14**	71	46
	5			45	25	31	**4**	**–20**	–32
	6			44	**17**	42	**18**	**–18**	–26
1990	7				**–8**	**–1**	29	**–14**	**–13**
	8				**–14**	**–12**	26	–23	**–15**
	9				**–8**	**–14**	22	–38	–25
1991	10					**–1**	29	**–13**	**13**
	11					**–9**	25	**–18**	–26
	12					**–8**	35	**–11**	**–4**
1992	13						**–3**	23	23
	14						**5**	22	28
1993	15							–46	–63
	16							–57	–73
	17							–43	–40
1993	18							**–12**	–28
Revised	19							–32	–33
	20							**1**	**–9**
	21							**–6**	**–17**
1994	22								**9**
	23								**–10**

as a proxy for water temperature, was negatively correlated with Tortugas pink shrimp landings during the following July–September. The present analyses for the Tortugas fishery rarely included air temperature as a predictor variable, perhaps because predictors were limited to the warmest months of May–October. Costello and Allen (1970) listed no known negative impacts of high summer temperatures on pink shrimp. Air and water temperature have been found to be potential predictors in a variety of other fisheries (Fogarty, 1989).

One final type of data consistently entered my models, i.e. September wind speed at Key West. Wind speed and direction were postulated by Vance et al. (1985) to affect recruitment and settlement of postlarval *Penaeus merguiensis* and thus subsequent harvest. Off Florida, high winds in September, associated with passage of tropical storms, could break up advective processes that deliver planktonic pink shrimp to the nursery areas during the summer. However, concurrent studies of oceanographic features and larval pink shrimp abundance remain to be conducted during this period (Criales and Lee, 1995). It is also possible that high winds in September reduce fishing effort and thus subsequent harvest, but high winds occur during the low point of the fishing year.

My forecasting method involves generating new prediction equations each year, rather than employing a single fixed equation, because 1) the models do not describe cause and effect relationships, 2) causal relationships between most variables and subsequent recruitment to the fishery are not well known (leading to the "hazards of correlative studies" noted by

Hannah (1993), and references cited therein), and 3) changes occur in the database used to make predictions. In time, new environmental, biological, or fishery conditions are encountered. For example, the database for the Tortugas pink shrimp fishery now reflects (directly or indirectly) results of massive seagrass mortality in Florida Bay which began in 1987, a prolonged drought in south Florida during 1989–91, and the four worst fishing years on record. None of these factors would have influenced the first forecast model derived in 1987, and assessment of that model indicated it would have been a failure if used in most future years. Even the durable Texas brown shrimp forecast, first released to the public in 1962 and accurate within ±20% of actual landings for 22 of its first 29 forecasts, was modified in 1994 to reflect the changing nature of the Galveston Bay live bait shrimp fishery after 1980.[2]

Incorrect fishery forecasts can have negative economic impacts on fishermen and processors (Bocking and Peterman, 1988; Walters, 1989), especially if the fishery in question is actively regulated on a short-term basis like the salmonid fisheries of the northeastern Pacific. The penaeid shrimp fisheries of the U.S. Gulf of Mexico are managed to prevent the harvest of undersized shrimp (Gulf of Mexico Fishery Management Council, 1981; Klima et al., 1986). Shrimp management strategies are assessed annually and are accomplished by seasonal closure of Federal and state waters off Texas and by areal closure of shallow Federal waters off southwest Florida. Flexible, in-season adjustments are possible but rare, and to date shrimp management has not been altered in response to forecasts of high or low harvests. As yet, no assessment of the utility and economic effects of either pink shrimp or brown shrimp forecasts have been made among members of the fishing community.

This study indicates that landings of Tortugas pink shrimp might be forecast reliably with some advance knowledge of environmental conditions and abundance of juvenile pink shrimp in nursery areas. Cause-effect relationships are not yet known, and mechanisms describing pink shrimp responses to predictor variables need to be determined through experimental analyses.

Acknowledgments

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Energetics of larval red drum, *Sciaenops ocellatus.* Part I: Oxygen consumption, specific dynamic action, and nitrogen excretion

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Abstract.—Oxygen consumption and nitrogen excretion rates were determined by direct measurement in fed and starved red drum, *Sciaenops ocellatus*, larvae between the ages of two and eighteen days. Oxygen consumption rates (Y, μL O_2/ind./h) scaled isometrically with mass (X, mg) according to the equation $Y = 4.58X^{1.04}$ (r^2=0.80) in larvae fed 5 prey/mL, resulting in a dry mass-specific oxygen consumption (QO_2) of 4.18 μL O_2/mg DM/h at a mass of 100 μg. In contrast, oxygen consumption of starved larvae scaled with mass according to the relationship $Y = 1.00X^{0.697}$ (r^2=0.50), resulting in a QO_2 of 2.01 μL O_2/mg DM/h at 100 μg. The 50% drop in QO_2 between fed and starved larvae over the mass range addressed in the study was assumed to represent the metabolic cost of growth (specific dynamic action).

Nitrogen was excreted in the form of ammonia and urea. Ammonia excretion (Y, μg NH_3/ind./h) varied with mass (X, mg) in fed individuals according to the relationship $Y = 0.277X^{0.728}$ (r^2=0.58), resulting in a dry mass-specific ammonia excretion rate of 0.52 μg NH_3/mg DM/h at a mass of 100 μg. Like oxygen consumption, nitrogen excretion in starved individuals dropped to 50% of that in fed animals, suggesting a general metabolic slowdown during starvation. Urea production as a percentage of total N-excretion was inversely related to ammonia production in starved individuals and increased with time of starvation; it may be an indicator of starvation in very young fish.

The isometric scaling of metabolism with mass in young larvae suggests that physiological vulnerability, i.e. susceptibility to starvation, does not decline rapidly with increasing size in young fish larvae. Larger larvae are nearly as vulnerable to starvation as smaller ones though their ecological position has improved, i.e. their predator spectrum has declined and their prey spectrum has increased.

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Energy utilization during a fish's early life history reflects its strategy for survival. Ingested energy must be apportioned between metabolic requirements and the need for growth in size; the remainder is lost as fecal and nitrogenous waste. The need for rapid growth in very young larvae is particularly critical: increasing size rapidly decreases the spectrum of potential predators even as it increases the spectrum of items available for forage (Weatherly and Gill, 1987). The two factors that most profoundly influence the amount of ingested energy available for growth are the energy lost to respiration and excretion (Brett and Groves, 1979; Houde, 1989).

Respiration in eggs and larvae is believed to occur through cutaneous diffusion (de Silva, 1974). At hatching, most species of fish lack respiratory pigments and are almost transparent. The blood of these larvae becomes pink weeks or months later upon transformation, which marks the time of blood pigment development and advanced gill filament formation (Weihs, 1981; Blaxter, 1986). Energy demands of respiration in fish larvae are temperature-dependent, ranging from 48% of the gross ingested food energy at 10°C to 31% at 30°C (Houde, 1989).

A portion of the food energy ingested by an individual is indigestible and lost as feces (up to 20% in older fish; Brett and Groves, 1979). In larval fishes, feces are small, difficult to collect, and, as a consequence, are rarely measured. The fraction of ingested energy lost to fecal excretion is therefore usually computed by the difference between the sum of the energy devoted to growth and metabolism and that ingested. Of the remaining food energy that is digestible, a portion is lost as nonfecal nitrogen, mainly as ammonia and urea. Brett and Groves (1979) have stated that energy lost through nonfecal excretion ranges from 3% to 10% of total ingested calories in adults. However, data describing nitrogen excretion in young fish larvae are very scanty. Available figures suggest that total excretion ranges from 23% to 40% of the gross ingested energy (Houde, 1989).

Data collected simultaneously on oxygen consumption and ammonia excretion can be used to determine the biological substrate that is combusted as fuel by using the atomic ratio of oxygen consumed to nitrogen produced (O:N ratio) (Davenport et al., 1983). The O:N ratios of 8 or less indicate that pure protein

is being combusted. Values higher than 20 suggest that lipids are the primary source of energy (Bayne, 1973). Larvae depleting their yolk-sac lipid reserves should thus exhibit high O:N values, whereas fast-growing larvae actively synthesizing protein with little or no lipid deposition or combustion should have low O:N values.

The aims of this study were to determine the respiratory costs of red drum larvae in their first 2 weeks of life, to determine the amount of energy lost as nitrogenous waste in the form of ammonia and urea, to determine the effects of starvation on both nitrogen excretion and respiration, and to determine, by using O:N ratios, the main biological fuel being combusted for energy.

Methods and materials

Maintenance of specimens

Fertilized eggs were obtained from the Florida Department of Environmental Protection (FDEP) hatchery in Port Manatee, Florida. Broodstock was maintained at a temperature of 25°C and a salinity of 30‰. Eggs were obtained from six spawnings over the course of six months to complete the respiration and excretion experiments described below.

Eggs were transported to the University of South Florida Marine Science Laboratory in St. Petersburg, and 2,500–3,000 individuals were placed into each 26-L experimental aquarium. The high mortality associated with first-feeding (cf. Roberts et al., 1978) resulted in a concentration of 250–300 individuals per aquarium after the first 3 days of life. Aquaria were kept in a photoperiod- and temperature-controlled incubator; water was maintained at 25°C and 30‰. A 13-hour light and 11-hour dark photoperiod was used throughout all experiments. Larvae were fed rotifers (*Brachionus plicatilis*) starting at day 3 after hatching until transformation (approximately day 14), when experiments were terminated. Aquaria were aerated and 10% of the water in each was changed daily.

Rotifers were cultured by using the procedure of Hoff and Snell (1987). Seawater for culturing was obtained from offshore in the Gulf of Mexico. The seawater was coarse-filtered, treated with bleach (sodium hypochorite, 5.25%) to remove any additional plankton, and neutralized with sodium thiosulfate. Salinity was adjusted with distilled water and Tropic Marine Seasalt to achieve a final salinity of 30‰.

Rotifers were provided at 5.0 per mL from first feeding (day 3) through day 14. Prey concentrations were monitored twice daily by removing a 25-mL sample from each aquarium, counting the number of prey in 0.5-mL aliquots, and taking the average. Concentrations were adjusted to maintain prey concentrations as necessary.

Oxygen consumption rate

Oxygen consumption was measured in red drum larvae ranging in age from 3 to 18 d. Individuals used in respiratory determinations were of two types: those fed ad libitum and those that had been starved for 24 h. Oxygen partial pressure was monitored in respiratory chambers with both "micro" and "needle" polarographic oxygen electrodes (Mickel et al., 1983; Revsbech and Ward, 1983) as individuals or groups of individuals reduced the oxygen levels to low (0–40 mm Hg) partial pressures. Cathode diameters on both the micro- and needle electrodes were sufficiently small to preclude the need for stirring; both types were manufactured in our laboratory. Starved individuals were monitored with the needle electrodes and fed larvae were monitored by both micro and needle electrodes. Electrodes were calibrated before and after each experimental run with air- and nitrogen-saturated seawater.

Respiratory chambers were manufactured from plastic 1-mL and 10-mL syringes. Each chamber was filled with seawater filtered through a 0.45 μm millipore filter and capped with an electrode fitted with an O-ring. The respiratory chamber within the syringe barrel was thus defined at one end by the syringe plunger and at the other end by the oxygen electrode. Single individuals were run by using a 1-mL syringe and the needle electrode set-up. Groups of 2 to 4 individuals were run in 10-mL syringes with a micro-electrode. Chambers were kept at 24 (±1.0)°C.

Data were continuously recorded throughout each run with either a computer-controlled data logging system (micro-electrodes) or a chart recorder (needle electrodes) (Donnelly and Torres, 1988). For data acquired with the chart recorder, the oxygen consumption rates were computed directly from the slope of the recorded data. Rates were calculated from the data-logger by noting the oxygen depletion over 10-min intervals. Typically, the first 30 min of a run were characterized by a high rate because of excitement associated with introduction into the respirometer. Thus, in all cases, data acquired during the first 30 min of the run were discarded. A mean respiratory rate for each run was determined by taking a mean of all the 10-minute rates comprising the run after the first 30 min. The lowest and highest 10-min rates for each run were designated the minimum and maximum rates.

After each run, individuals were rinsed with distilled water and dried at 60°C for 24 h, then weighed

with a Cahn Electrobalance for dry mass measurements. It should be noted that the number of replicate experiments for larvae starved for 24 h was lower than that for fed individuals because many of the larvae that survived the period of starvation were not hardy enough to be good experimental subjects.

Oxygen consumption as μL O_2 was converted to calories (cal) by using the oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves, 1979). Calories were then converted to joules (J) by multiplying by 4.1868 J/cal (Pennycuick, 1988).

Nitrogen excretion

Nitrogen excretion rates were determined for larvae of the same ages and feeding states as those used in the oxygen consumption experiments. Larvae aged 3 to 14 d were split into 2 feeding groups: those fed to satiation and those starved for 24 h. Five sets of 10 larvae were removed from each feeding group and each set was placed in a 10-mL screw-top centrifuge tube filled with seawater that had been filtered through activated charcoal. To measure any ammonia addition caused by transfer of the larvae, an additional tube was filled with charcoal-filtered seawater, and a volume of water from the incubation bowl equivalent to that associated with transfer of the larvae was added. A second additional tube was filled with 10 mL of charcoal-filtered seawater to serve as a blank.

All tubes were sealed and incubated for 4 h at 25°C. Larvae were subsequently filtered from the tubes with 50-μm mesh netting, dried at 60°C for 24 h, and weighed. The remaining sample water was split into 10-mL aliquots and immediately capped and frozen for later analysis. Concentrations of ammonia and urea for each sample were determined colorimetrically with an Alpkem autoanalyzer (Price and Harrison, 1987).

O:N ratios

O:N ratios (mol/mol) were calculated by using mass-specific oxygen consumption rates and our data for mass-specific total nitrogen excretion (ammonia and urea). Rates of mass-specific ammonia excretion were used to obtain O:NH_3 ratios.

Results

Oxygen consumption rates

Absolute oxygen consumption rates for individuals (ind.) fed 5.0 rotifers/mL increased with increasing dry mass and, as a consequence, with the age of the larvae as well (Table 1: Fig. 1). Rates ranged between 0.05 (day 3) and 0.14 μL O_2/ind./h (day 7) for the first week of growth. During the second week of growth, values increased sharply from 0.14 to 0.34 μL O_2/ind./h at day 14, reaching 0.77 μL O_2/ind./h at 18 d after hatching. The slope (b) of the oxygen consumption versus mass curve was 1.04 ±0.08 ($\bar{x}$ ±SE), indicating that metabolism was directly proportional to mass (isometric scaling) for the first two weeks of life. Mass-specific oxygen consumption (QO_2) varied between 2 and 6 μL O_2/mg DM/h with a mean of 4.23 ±0.17 μL O_2/mg DM/h ($\bar{x}$ ±SE). The slope (b) of the regression line for oxygen consumption versus age was 1.28 ±0.12.

Individuals starved for 24 h also had absolute oxygen consumption rates that increased with mass and age, but with lower b values (Fig. 2). Slope (b) for the oxygen consumption vs. mass curve dropped to 0.697 ±0.230 ($\bar{x}$ ±SE); that for oxygen consumption vs. age dropped to 0.975 ±0.400 ($\bar{x}$ ±SE). Absolute and mass-specific oxygen consumption and, as a consequence, energy utilization of starved larvae was one-half or less that of fed larvae at all ages up to day 17 (Table 2).

Table 1

Oxygen consumption of red drum, *Sciaenops ocellatus*, larvae fed at 5.0 prey/mL. n = number of sample runs; MDM = mean dry mass in μg; QO_2 = mass-specific oxygen consumption in μL O_2/mg DM/h; and ( ) = standard deviation.

Day	n	MDM	μL/ind./h	Mean QO_2	Min QO_2	Max QO_2
3	6	17.0	0.0473	2.78 (0.93)	1.15 (0.43)	4.56 (0.65)
4	4	24.1	0.1128	4.68 (1.02)	2.54 (1.38)	7.48 (1.71)
7	2	31.5	0.1402	4.45 (2.59)	1.53 (1.35)	11.70 (3.30)
8	4	34.1	0.1238	3.63 (1.73)	1.35 (1.17)	8.28 (2.79)
9	8	46.1	0.2466	5.35 (1.47)	2.01 (1.13)	11.10 (6.27)
10	5	52.0	0.2844	5.47 (0.83)	3.22 (1.46)	8.91 (3.85)
12	6	68.6	0.2593	3.78 (1.94)	1.24 (0.33)	10.80 (2.79)
14	6	109.0	0.3412	3.13 (1.56)	1.20 (0.54)	8.08 (3.18)
17	2	155.0	0.7316	4.72 (2.63)	1.46 (0.05)	12.40 (7.61)

Nitrogen excretion rate

Absolute ammonia excretion rates (Y, µg/ind./h) increased with increasing mass (X, mg) in larvae fed to satiation according to the relationship $Y = 0.277X^{0.728}$ (r^2=0.58) (Fig. 3). The slope of the excretion vs. mass curve in fed larvae (0.728) indicates that mass-specific ammonia excretion declines with increasing mass.

The relation between ammonia excretion and mass was substantially changed with a 24-h period of starvation, such that $Y = 0.058X^{0.328}$ (r^2=0.40) (Fig. 4). The change indicates that absolute ammonia excretion in starved individuals is roughly 50% that of fed individuals. In addition, the decline in mass-specific ammonia excretion with increasing mass is more pronounced as is indicated by the lower slope (0.328).

The increasing mass of growing larvae fed to satiation resulted in an increase in absolute ammonia excretion with age (Fig. 3). Starvation resulted in about a 50% decline in the slope of the relationship between excretion and age, similar to that observed in excretion vs. mass.

The percent contribution of ammonia and urea to total excretion differed; urea dominated in starved individuals. Urea in starved larvae (as total N excreted) was twice that of fed larvae (Table 3).

O:N ratios

The low O:N ratios based on both ammonia-N (O:NH_3) and total nitrogen (ammonia-N and urea-N) excretion rates indicated that protein was the combusted fuel (Table 4). O:NH_3 ratios ranged between 4 and 12 for all ages. O:N values based on combined ammonia-N and urea-N excretion were lower, ranging between 1 and 9. Larvae starved for 24 h

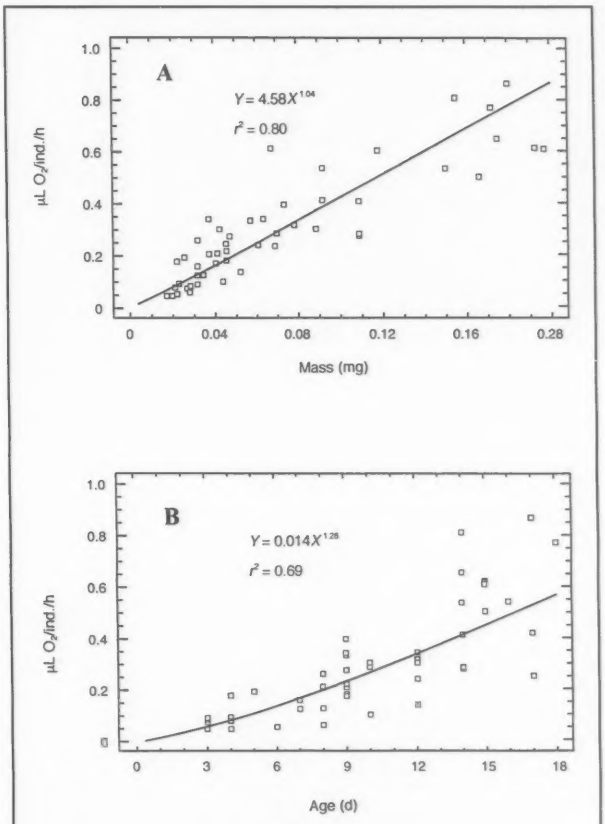

Figure 1

Absolute oxygen consumption (µL O_2/ind./h) in red drum, *Sciaenops ocellatus*, larvae fed to satiation as a function of (**A**) dry mass (mg) and (**B**) age (d).

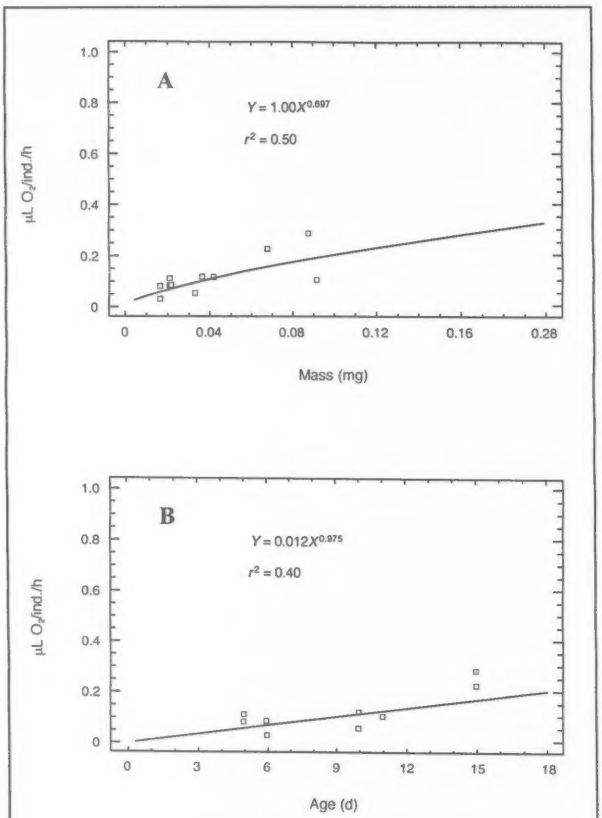

Figure 2

Absolute oxygen consumption (µL O_2/ind./h) in red drum larvae starved for 24 hours as a function of (**A**) dry mass (mg) and (**B**) age (d).

had lower O:N ratios than fed larvae on days 6 and 10. Starved larvae had O:NH_3 ratios between 4.3 and 12.0 and O:N ratios between 1.7 and 9.0.

Discussion

Oxygen consumption rates

Absolute oxygen consumption of red drum larvae was similar to that reported for other larval fishes. Fyhn and Serigstag (1987) found absolute oxygen consumption rates of 0.05–0.100 µL O_2/ind./h in cod larvae for the first 5 d of life at 5°C, which, despite the differences in species and temperature, were similar to our results for red drum. A comparison with other subtropical species is offered by the data of Houde (1983) who reported rates of 0.08 to 0.14 µL O_2/ind./h for 25.5 µg-sized sea bream, *Archosargus rhomboidalis*, reared at 26°C, increasing to 0.44–0.62 µL O_2/ind./h in 41–66 µg individuals. Values for red drum

Table 2

Energy allocated to feeding metabolism of red drum larvae during the first two weeks of life. J = joule.

Age (d)	Fed rate (J/ind./h)	Starved rate (J/ind./h)	% reduction
3	0.0015	0.0008	46.7
4	0.0017	0.0010	41.2
6	0.0024	0.0013	45.9
10	0.0044	0.0021	52.2
14	0.0083	0.0033	60.2

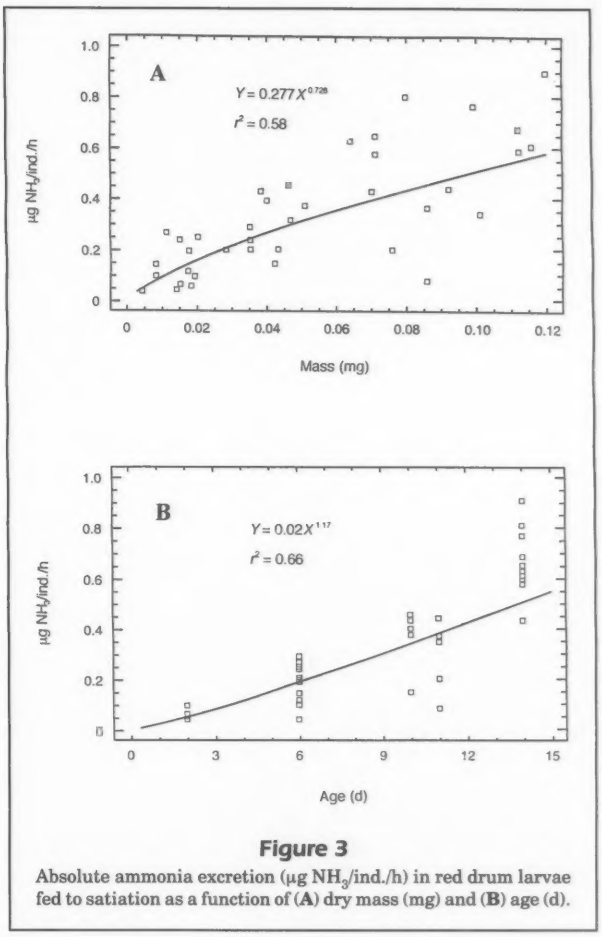

Figure 3

Absolute ammonia excretion (µg NH_3/ind./h) in red drum larvae fed to satiation as a function of (**A**) dry mass (mg) and (**B**) age (d).

larvae were lower at 0.05–0.14 µL/ind./h for 21–31 µg fish and 0.26–0.28 µL/ind./h for 52–68 µg larvae.

The regression of absolute oxygen consumption versus mass in larval red drum conformed to the equation $Y = aM^b$ (Fig. 1) and had a slope or "*b* value" of 1.04 (±0.08), which is greater than the most widely used figure of 0.75 (Schmidt-Nielsen, 1983), and the slope of 0.80 commonly cited for adult fish (Brett and Groves, 1979; Houde, 1983; Prasad, 1986). The slope of 1.04 (±0.08) exhibited by red drum larvae indicates that oxygen consumption scaled directly with body mass (1.0) rather than with surface area (0.67). It is becoming increasingly apparent that metabolism scales isometrically with mass in larval fishes (see review by Giguere et al., 1988); thus, a *b* value of 1.0 is the norm rather than the exception for larval fishes and most likely for larval forms in general (Manahan, 1990).

Feeding metabolism

Oxygen consumption rates for two-week-old red drum starved for 24 h declined to about 50% of those for fed individuals (Table 2), which is within the range reported in larval starvation studies with several other species (Holliday et al., 1964; Giguere et al., 1988; Tucker, 1989). The reduction of oxygen consumption in starved versus fed individuals reflects the decrease in energy expenditure associated with feeding metabolism, otherwise known as specific dynamic action (SDA) (Kleiber, 1961; Kiørboe et al., 1985; 1987; Kiørboe, 1989). Jobling (1981a, 1983) suggested that SDA represents the energy expenditure associated with growth. His arguments may be summarized as follows. Biosynthesis is an energy-requiring process (Lehninger, 1985). As a consequence, some fraction of the adenosine triphosphate

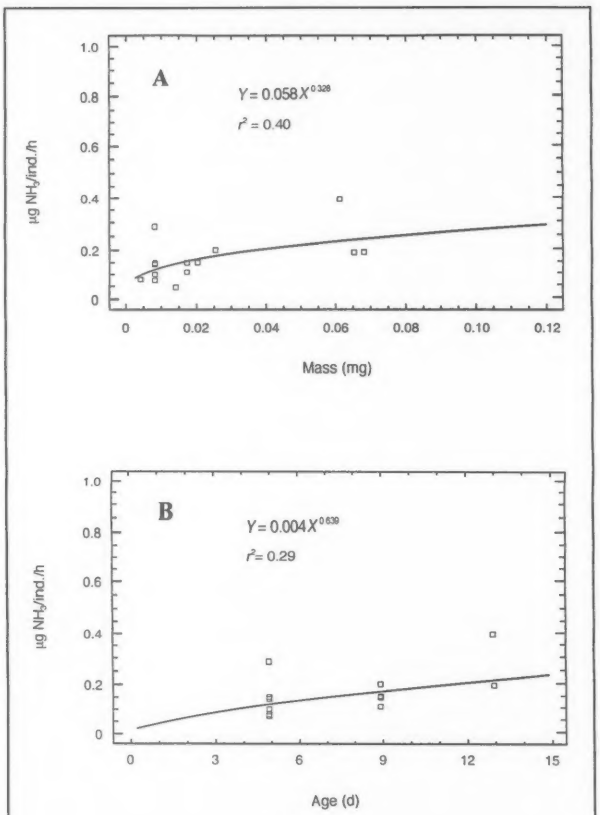

Figure 4

Absolute ammonia excretion in red drum larvae starved for 24 hours as a function of (**A**) dry mass (mg) and (**B**) age (d).

(ATP) generated by aerobic metabolism must be used for growth in a normal, developing individual. The fraction of aerobic metabolism that generates the ATP for biosynthesis is the increase in metabolism following feeding variously known as specific dynamic action (SDA) (Kleiber, 1961), specific dynamic effect (Kleiber, 1967), or heat increment (Brett and Groves, 1979). Thus, diets that promote high growth induce high energy use as SDA. Jobling's view conflicts with the more traditional idea that growth and SDA are in direct competition for ingested energy.

The 40% to 60% reduction in metabolic rates of starved individuals indicates that feeding metabolism (SDA) is a substantial fraction of the daily metabolic costs above maintenance in fed larvae. Because SDA is specifically related to growth, and individuals growing slowly demonstrate little change in metabolic rate following feeding (Jobling, 1985), it follows that the large reduction in metabolic rate of starved red drum is indicative of a rapidly growing fish.

Nitrogen excretion

Our data on nitrogen excretion are the first reported for larval red drum; they add significantly to the very limited information describing excretion in fish larvae. Absolute ammonia excretion rates of red drum larvae (Table 3; Fig. 3) were similar to those reported by Klumpp and von Westernhagen (1986) for similar size *Pleuronectes platessa* (0.025–0.050 µg NH_3/ind./h at 100 µg and 11 d) and *Blennius pavo* (0.05–0.10 µg NH_3/ind./h at 100 µg and 5 d).

The 50% drop in absolute and mass-specific ammonia excretion with starvation (Table 3; Figs 3 and 4) mirrors the drop observed in oxygen consumption rate, indicating a general slow-down in metabolic

Table 3

Mean ammonia and urea excretion in red drum larvae fed to satiation and starved for 24 h. n = the number of samples (10 fish per sample); * = 24 h starved; ( ) = standard deviation.

Age (d)	n	Ammonia µg/ind./h	Ammonia µm/ind./h ($\times 10^{-3}$)	Urea µm/ind./h ($\times 10^{-3}$)	Excretion % urea
2	5	0.006 (0.001)	0.325 (0.20)	0.0793 (0.08)	32.8
6	10	0.023 (0.007)	1.333 (0.38)	0.2058 (0.03)	23.6
6*	10	0.016 (0.008)	0.660 (0.20)	0.4648 (0.11)	58.5
10	10	0.038 (0.012)	2.215 (0.40)	0.3038 (0.03)	21.5
10*	5	0.015 (0.004)	0.883 (0.23)	0.6678 (0.85)	60.2
14	10	0.067 (0.013)	3.918 (0.78)	0.4205 (0.04)	17.7
14*	5	0.039 (0.001)	2.265 (0.07)	0.4160 (0.25)	32.7

Table 4

Molar oxygen:nitrogen ratios for red drum larvae fed to satiation, and those starved for 24 and 48 h. ( ) = Standard deviation; * = starved 24 hours.

Age (d)	Oxygen (µm/mg/h)	Ammonia (µm/mg/h)	Urea (µm/mg/h)	O:NH_3	O:N
2	0.244 (0.021)	0.024 (0.005)	0.006 (0.005)	10.16 (2.44)	6.78 (1.49)
6	0.367 (0.183)	0.084 (0.039)	0.013 (0.002)	4.37 (3.12)	3.37 (3.02)
6*	0.401 (0.087)	0.089 (0.039)	0.063 (0.014)	4.51 (1.74)	1.86 (0.63)
10	0.598 (0.183)	0.050 (0.018)	0.006 (0.001)	11.96 (2.07)	9.65 (1.70)
10*	0.189 (0.062)	0.044 (0.006)	0.033 (0.004)	4.30 (0.58)	1.72 (0.26)
14	0.321 (0.091)	0.049 (0.008)	0.005 (0.001)	6.55 (1.64)	5.44 (1.37)
14*	0.288 (0.005)	0.024 (0.012)	0.004 (0.003)	12.00 (0.18)	9.00 (0.12)

processes with starvation. As was demonstrated by the O:N ratios (see below), the normally fast-growing young larvae apparently combust their own tissues to fuel their metabolic needs.

Values obtained in the present study for the percentage of nitrogenous waste in the form of urea agree well with previously reported values. Jobling (1981b) found that 15% to 25% of nitrogenous waste in plaice larvae occurred in the form of urea: his values agree well with our values of 18% to 33%. Ammonia as a percent of the total nitrogen excretion increased with age in red drum larvae fed to satiation.

Production of urea may play a role in survival of young larvae. Griffin (1991) proposed that urea synthesis was a mechanism for detoxifying ammonia during early embryogenesis, particularly before hatching, and several investigators have reported the presence of urea-cycle enzymes in larval fish (Rice and Stokes, 1974; Dépêche et al., 1979; Anderson, 1995). Urea costs more energy to produce than ammonia, but it is less toxic. It is used extensively in osmoregulation by elasmobranchs (Anderson, 1995), as an excretory product to prevent poisoning during estivation by African lungfish (Janssens, 1964), and in response to elevated external ammonia levels or to stress in toadfish (Walsh et al., 1990). It is possible that production and retention of urea in young red drum larvae could be used to increase blood osmolarity, in a manner similar to that of elasmobrachs, to aid in osmoregulation. Alternatively, it may be a response to the stress of starvation.

The percent increase in urea production with starvation has been observed in other fishes under hatchery conditions (Brett and Zala, 1975). The constant mass-specific nitrogen excretion in starved fish, despite the changes in relative contributions of ammonia and urea, is indicative of continued protein catabolism. However, the protein catabolized in starved individuals was the protein contained within the larva's own tissues.

Urea normally contributes less than 50% of the total nitrogen excreted and is often overlooked, but the results here suggest urea is an excellent indicator of starvation in larval fishes. The decrease in

percentage of urea excreted by larger red drum larvae could indicate a metabolic shift away from urea production in larvae approaching transformation or in the secondary loss of the ability to produce it (cf. Anderson, 1995).

O:N ratios

Nitrogen excretion data for larval red drum suggest that protein was the major catabolic substrate, with little, if any, energy being stored in, or produced from, lipid reserves. Low O:N ratios in well-fed red drum larvae as well as in those starved for 24 h indicated a protein fuel source in all cases. Ingested rotifers were protein-rich (Brightman, 1993) which almost certainly contributed to the low O:N ratios of fed individuals. The slightly lower O:N ratios for starved larvae suggest an even stronger dependence on protein for metabolic fuel, combusted at the expense of tissue protein.

Conclusions

An interesting outgrowth of the present study is not only the amplitude of change in metabolism with starvation, but the change in the scaling coefficient as well. The drop in "*b*" from 1.04 to 0.697 as a result of starvation suggests that the larger larvae have sustained a proportionately greater drop in metabolism than the smaller ones, which, in turn, underscores a metabolic "catch-22" situation in young larvae. Rapid growth of a larva decreases the number of its potential predators, thereby giving the larva the ecological refuge of increased size. In addition, it simultaneously increases the size range of its potential prey. However, the fact that metabolism scales directly with mass means that larger larvae will also be combusting more metabolic fuel in an absolute sense than will smaller individuals. Because energy storage in red drum larvae is almost nonexistent (Brightman, 1993), the absolute metabolic costs of being larger could prove to be rapidly debilitating during times of starvation (cf. Giguere, 1988). In juvenile and adult fishes, "*b*" values typically are close to 0.80 (Giguere, 1988) and weight-specific oxygen consumption declines with increasing size. Thus, in adult fish, larger size gives a metabolic refugium as well as an ecological one. Because larger adults have a proportionately lower metabolism than smaller adults, starvation will be proportionately less debilitating for the larger fish. Thus, the "catch-22" of isometric scaling (b=1.0) in the very early life history of fish is that it is almost certainly part of the metabolic underpinnings of rapid growth, but it also makes larger larvae nearly as vulnerable to starvation as smaller ones. Rapid growth gives an ecological refuge but it comes at the expense of physiological vulnerability.

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Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event, 1991–1993

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Abstract.—Rockfish are among the most prevalent members of nearshore ichthyoplankton assemblages off central California, yet their abundance varies greatly from year to year. Warm events, like El Niño, can have pronounced effects on the success of a year class. We evaluate distribution, abundance, and species composition of rockfish larvae on small spatial and temporal scales in the upwelling center north of Monterey Bay during an extended El Niño (December 1991 through June 1993) relative to regional hydrography.

Anomalously warm, low-salinity water to depths greater than 50 m during much of our study was indicative of an onshore displacement of the California Current. Upwelling was reduced and delayed relative to other years. The two years differed, however, in the intensity, duration, frequency, and direction of wind events. Larval rockfish abundance was similar in both years of the El Niño, peaking in early February, and was among the highest when compared with estimates from CalCOFI surveys off central California (1951–84). Using larval ages, we determined that median birthdates of shortbelly rockfish were in early- to mid-February both years. Growth rates of larval shortbelly rockfish did not differ among months or between years. Relative to 1993, rockfish larvae were more abundant, and sizes of larval shortbelly were significantly greater at onshore stations in 1992. This coincided with onshore advection of water during the onset of the El Niño, suggesting retention of larvae nearshore. Initiation of upwelling in March and April 1993 and fewer larvae at onshore stations are indicative of greater offshore transport during the second year.

Juvenile rockfishes were extremely rare in summer of 1992; in 1993 they were twenty times more abundant and larger. Surviving juvenile shortbelly rockfish were born late during both years; upwelling occurred coincidentally during this period in 1993 but not in 1992. We suggest that substantially higher survival and recruitment of juvenile rockfishes in 1993 was due to increased offshore transport and perhaps lower predation during the larval stages.

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Ocean conditions off central California are influenced seasonally by a variety of factors and processes that operate on a local scale (e.g. wind, upwelling, freshwater input, and bathymetry) and larger spatial scales (e.g. the California Current System and El Niño events). Prevailing winds from the northwest produce relatively intense upwelling, particularly near capes and headlands, typically during March through September (Kelly, 1985; Breaker and Broenkow, 1994; Rosenfeld et al., 1994a). An abrupt decrease in sea-surface temperature, occurring sometime between February and May, defines the spring transition to coastal upwelling, which is associated with increased nutrient concentration, primary production, and offshore transport of surface water. Because the coastal ocean environment can respond rapidly to changes in local wind speed, direction, and duration, onshore transport of water off central California can occur during periods of reduced equatorward winds and subsequent cessation of upwelling (Broenkow and Smethie, 1978; Rosenfeld et al., 1994a). This transport is manifested nearshore by the occurrence of warm, relatively low salinity water representative of the offshore core of the California Current.

Point Año Nuevo (37.1°N, 122.3°W), to the north of Monterey Bay, has been identified as a distinct center of upwelling, associated with bifurcated plumes of cool, saline, nutrient-rich surface water that are advected both seaward and southward across Monterey Bay (Tracy, 1990; Schwing et al., 1991; Rosenfeld et al., 1994a). According to satellite and in situ data, these recurrent upwelling plumes can extend 10–100 km offshore and persist from days to weeks. As it flows equatorward, some of this upwelled water is advected into the bay.

Rockfishes (*Sebastes* spp.) are tremendously diverse, dominate coastal benthic fish assemblages and support heavily exploited recreational and commercial fisheries in California (Lea, 1992). Although rockfish larvae are among the most prevalent members of nearshore ichthyo-

plankton assemblages, especially off central California, annual abundance varies widely (Moser and Boehlert, 1991; Moser et al., 1993). Factors affecting survival of young fishes, including hydrographic conditions and associated transport processes, density of prey and predators, and spawning seasonality are potentially critical determinants of rockfish recruitment.

Rockfishes are viviparous, with larval release (parturition) occurring mainly from January to April for many of the species off central California (Wyllie Echeverria, 1987), just before and during the onset of upwelling. Duration of the pelagic larval and juvenile stages of many species is typically several months (Anderson, 1983; Woodbury and Ralston, 1991) but may be up to one year (Boehlert, 1977). The arrival and subsequent settlement of pelagic juvenile rockfishes in subtidal areas off central California may be associated with upwelling events and onshore transport during periods of wind relaxation (VenTresca et al., 1990; Larson et al., 1994). The recurring bifurcated plumes of upwelled water off Pt. Año Nuevo, a relatively unfished area that could serve as a source of larvae, interspersed with occasional periods of wind relaxation and onshore transport, may be important vehicles for transport of young rockfishes from upwelling centers into nearshore areas of Monterey Bay and farther south.

Warm events, often indicative of an El Niño, occur along the coast of California every 2–10 years (Norton et al., 1985) and persist for 1–3 years (Chelton et al., 1982). Strong events occurred coastwide in 1926, 1941, 1958, and 1983 (Ware, 1995). El Niño-like conditions can include 1) increased sea-surface temperature (SST) and depth of thermocline; 2) positive sea-level anomalies (Chelton and Davis, 1982); 3) reduced upwelling, nutrients, and primary and secondary production (Fiedler, 1984; McGowan, 1985; Miller et al., 1985); and 4) increased poleward and onshore flow of coastal water (Simpson, 1984; Hayward et al., 1994; Lynn et al., 1995). Significant increases in SST were noted off central California during winters of 1972, 1976, 1979, and 1983, which corresponded with El Niño episodes (Breaker et al., 1983).

Warm events like, but not restricted to, El Niño can have disastrous effects on year-class strength of rockfishes, a group with arctic to temperate affinities and distribution (Karpov et al., 1995; Lenarz et al., 1995; Ralston and Howard, 1995). Anomalously warm water and suppression of upwelling have been associated with large-scale reductions in the primary prey (e.g. euphausiids and smaller zooplankton) of juvenile and adult rockfishes (Mullin and Conversi, 1989). Reduced prey abundance may negatively affect the somatic and reproductive condition of adult rockfish (Lenarz and Wyllie Echeverria, 1986; VenTresca et al., 1995), potentially disrupting the timing, location, and net output of reproduction. Changes in distribution and dispersal patterns of pelagic larvae, and altered production of their prey and predators, are expected during anomalous warm events (Bailey and Incze, 1985; Brodeur et al., 1985).

In this paper we evaluate distribution, abundance, and species composition of rockfish larvae and associated hydrography on small spatial (<20 km) and short temporal (biweekly to monthly) scales in an upwelling center north of Monterey Bay during an extended El Niño event (1991–93). From size, age, and estimated growth models, we compare birthdate distributions of early larvae and surviving pelagic juveniles of the most common species. We discuss potential larval transport and subsequent strength and timing of juvenile recruitment to nearshore areas along the central California coast.

Methods

Sampling

Ichthyoplankton surveys were conducted during daytime aboard the RV *Ricketts* (ca. 11 m long) at five stations along a northeast–southwest transect off Davenport, California (37°N, 122°10'W; Fig. 1). Sta-

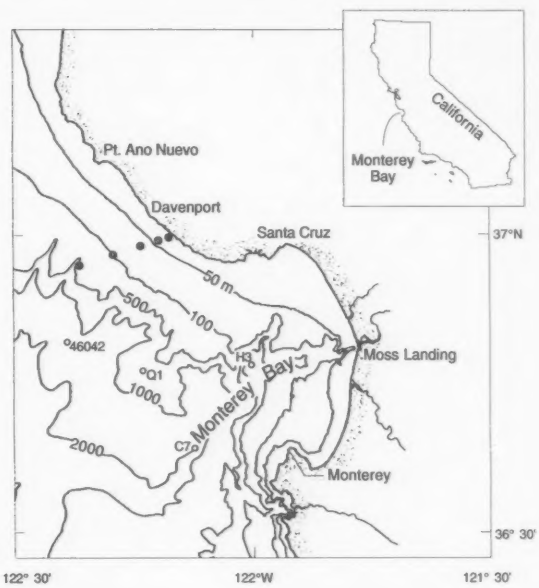

Figure 1

Monterey Bay study area and five stations (solid dots) sampled for larval fish off Davenport. Sites of wind measurements (46042) and 1989–91 CTD casts (H3, C7, and Q1) are indicated.

tions were located across the shelf at 1 km (15 m water depth), 3 km (30 m water depth), 7 km (60 m water depth), 13 km (100 m water depth), and 19 km (180–713 m water depth) from shore. During 1991–92, samples were collected at approximately two-week intervals from early December to April; less frequent sampling extended through June because of the absence of expected upwelling events during spring. Sampling between January and April 1993 was limited to monthly intervals by frequent storms and rough seas.

Larvae were sampled with two 70-cm (mouth diameter) open nets of 0.505-mm mesh, black Nitex fitted onto a bongo frame. Volume of water filtered (30–465 m^3 per net) was estimated from calibrated mechanical flowmeters positioned in the mouth of each net. Tows were made parallel to bathymetry at 1–3 k for 2–20 min (depending on depth) obliquely from near the bottom to the surface at nearshore stations and from 200 m to the surface at the offshore station. Three replicate tows were conducted at most stations (Table 1). Oceanographic data were collected from near bottom to the surface at each station with a calibrated CTD (conductivity, temperature, and depth) profiler (model SBE 19 SEACAT, Sea-Bird Electronics). Daily wind speed and direction during the survey period in each year were calculated from daily averages of east and north wind components measured at the National Data Buoy Center moored buoy 46042 (Fig. 1).

Table 1

Dates of collection and number of replicate oblique bongo net tows conducted along an onshore–offshore transect off Davenport, California, during winter–spring months of 1991–93. Stations are defined by bottom depth (m) and distance from shore (km). "—" indicates no samples were taken.

	Station depth (m)				
Date	15 (1 km)	30 (3 km)	60 (7 km)	100 (13 km)	200 (19 km)
1991–92					
02 December	3	3	2	3	3
18 December	3	3	3	3	3
09 January	3	3	3	3	3
23 January	3	3	3	3	3
06 February	3	3	3	3	3
21 February	3	3	3	3	3
12 March	3	3	3	3	3
02 April	3	3	3	3	3
04 May	—	—	—	1	1
16 June	—	3	3	3	—
Subtotal	24	27	26	28	25
1993					
29 January	3	3	3	3	3
12 February	—	—	3	3	3
07 March	—	3	—	—	3
06 April	—	3	—	3	3
Subtotal	3	9	6	9	12
Total	27	36	32	37	37

Plankton samples were preserved at sea, one sample from each bongo pair in 5% buffered formalin and the other in 80% buffered ethanol. Rockfish larvae were sorted under a dissecting microscope from each paired sample for all replicates per station. Formalin-preserved rockfish from all replicates were enumerated for abundance estimates. Only one ethanol-preserved replicate per station was processed for species identification. Standard length (or notochord length for preflexion larvae) was measured to the nearest 0.1 mm for shortbelly rockfish, *Sebastes jordani*, and blue rockfish, *S. mystinus*, preserved in ethanol. Otoliths were removed for age determination from a subsample of these two dominant species; larval ageing methods (i.e. counting daily growth increments in otoliths) followed Yoklavich and Bailey (1990). Within the otolith microstructure of larval shortbelly rockfish, a well-defined increment is formed at parturition, which has been adequately resolved with optical microscopy at 1250× magnification (Ralston et al., 1996). Daily formation of increments in otoliths has been demonstrated in juvenile black rockfish (*S. melanops*; Yoklavich and Boehlert, 1987) and in shortbelly and brown rockfish (*S. auriculatus*; Laidig et al., 1991).

Birthdates of larval shortbelly and blue rockfishes were calculated by using a linear growth model (e.g. fitted from the aged subsample) to estimate age from length and by subtracting age from date of capture. Birthdate distribution estimated from larvae was compared with that estimated from older pelagic young-of-the-year shortbelly rockfishes collected from May to July, 1992 and 1993, near Monterey Bay (see Loeb et al.[1] for details of surveys). Ages of these pelagic juveniles were estimated from length by using linear growth models developed for this species and size range collected from central California during May and June 1992 and 1993 (Woodbury[2]). Birthdate distributions were corrected for age-specific mortality across all daily cohorts with rates modified from

[1] Loeb, V. J., M. M. Yoklavich, and G. M. Cailliet. 1994. The importance of transport processes in recruitment of rockfishes (Genus *Sebastes*) to nearshore areas of Monterey Bay, California. Final Report, NOAA, California Sea Grant College, Project R/F-142, 25 p.

[2] Woodbury, D. 1996. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. data.

Ralston and Howard (1995): 0.1165, 0.10, 0.08, 0.06, 0.04, and 0.03/d for fish of age <15, 15–27, 28–42, 43–70, 71–100, and >100 d, respectively.

Larval identification

Preflexion and flexion rockfish larvae were identified primarily from melanistic pigment patterns, including: length of ventral midline series, occurrence of dorsal midline pigmentation, and occurrence of pectoral fin pigmentation. Distinctions among larvae with shared primary pigment patterns were based on secondary pigment characters (e.g. external dorsal midline pigment configuration, lower lip pigment, and pectoral fin size and pigment pattern), and on reproductive seasonality of adults (Wyllie Echeverria, 1987; Love et al., 1990).

Preextrusion, yolk-sac, and preflexion stages have been illustrated or described in some detail for 49 of the 52 species of rockfishes off central California (see Kendall [1991] for a general review). More advanced larval stages have been described for relatively few species of rockfish. We used serial descriptions of larvae from preflexion through flexion to identify shortbelly (Moser et al., 1977), blue (Moreno, 1993), cowcod (*S. levis*; Moser et al., 1977), bocaccio (*S. paucispinis*; Moser, 1967), and stripetail rockfish (*S. saxicola*; Laidig et al., 1996). All postflexion larvae with dorsal, anal, and pectoral fin rays were identified to species.

Squarespot rockfish, *S. hopkinsi,* were abundant as preflexion larvae and were identified cautiously from a description of their preextrusion stage (Moser et al., 1977). Two groups of species also were identified on the basis of shared pigment patterns. The "copper complex" informally is synonymous with the subgenus *Pteropodus* (Jordan et al., 1930; Kendall, 1991), and comprises copper (*S. caurinus*), gopher (*S. carnatus*), black-and-yellow (*S. chrysomelas*), grass (*S. rastrelliger*), china (*S. nebulosus*), and quillback (*S. maliger*) rockfishes. We include brown (*S. auriculatus*) and kelp (*S. atrovirens*) rockfishes in a "copper complex +" because their pigmentation is indistinguishable from members of *Pteropodus*. A "*Sebastosomus* +" group includes black, olive (*S. serranoides*), yellowtail (*S. flavidus*), widow (*S. entomelas*), and bank (*S. rufus*) rockfishes. Identification of this group is limited because yolk-sac and early preflexion larvae are indistinguishable from many other species, including most in the subgenus *Sebastomus*.

Data analysis

Larval abundance was calculated for each replicate at each station by multiplying the number of larvae by depth of tow and by dividing by the volume of water filtered per sample. Abundance was expressed as number of larvae per 10 m^2. Abundance data were examined for normality and were log-transformed where appropriate. Among-station and among-time differences in total abundance of larval rockfishes were tested for significance by using a 2-factor analysis of variance (ANOVA), including only those samples collected during the first eight periods in 1991–92 (i.e. those with three replicates per station and five stations per time period). Between-year comparisons of abundance were made with 2-factor ANOVA (i.e. factors were year and time) by using only those time periods and stations equally represented in both years. Specific time periods and stations that contributed to significant factors in the models were identified by using post-hoc pairwise multiple comparisons of cell means with Bonferroni-adjusted probabilities. Differences in mean size and growth rate of the two dominant species of larval rockfish among stations, collection times, and years were similarly analyzed.

Results

The physical environment

Our 1991–93 study period off central California was characterized by a prolonged El Niño event. Anomalously warm, low-salinity water in nearshore areas during much of our study indicated an onshore displacement of the California Current, similar to that reported by Lynn et al. (1995) for this time period and by Simpson (1984) for the 1982–83 El Niño event. Upwelling was reduced and delayed relative to other years, and distinct persistent upwelling plumes were not evident within the survey area during the sampling periods. The two years differed, however, in the intensity, duration, frequency, and direction of wind events that affected transport processes.

Coastal winds off Monterey prior to the 1991–93 El Niño event were primarily from the northwest during December to April (Fig. 2A), as estimated from daily wind components measured at buoy 46042 (Fig. 1) and averaged from 1988 to 1991. Associated with this prevailing wind pattern was a steady shoaling of cold, high salinity water, indicative of upwelling, in the upper 200 m of the water column in the outer part of Monterey Bay, as measured by a total of 37 CTD casts from stations H3, C7, and Q1 (Fig. 1) during April 1989, December 1989–April 1990, and December 1990–March 1991 (Fig. 2, B and C; raw data from Rosenfeld et al., 1994b).

During winter 1991–92, daily wind speeds were largely greater than the average calculated during

the same period from 1988 to 1991, but wind direction reversed in late December and the greater part of February and March 1992, blowing predominantly from the southeast for 2–12 d at a time (Fig. 3A). Coincidentally, water in the upper 80 m was warmer and fresher following these periods of southeast winds (Fig. 3, B and C); water of 15°C and 33.2‰ occurred near the surface by 2 April. Contoured vertical sections of temperature during the spring ichthyoplankton surveys off Davenport in 1992 indicated an increasingly stratified and warm water column at least to 19 km offshore (Fig. 4A); isohalines were similarly stratified. There was no evidence of upwelling (i.e. no shoaling of isotherms and isohalines near the coast) during winter–spring 1992. For comparison with the following year, note that the 10°C isotherm remained below 100 m during the 1992 sampling season.

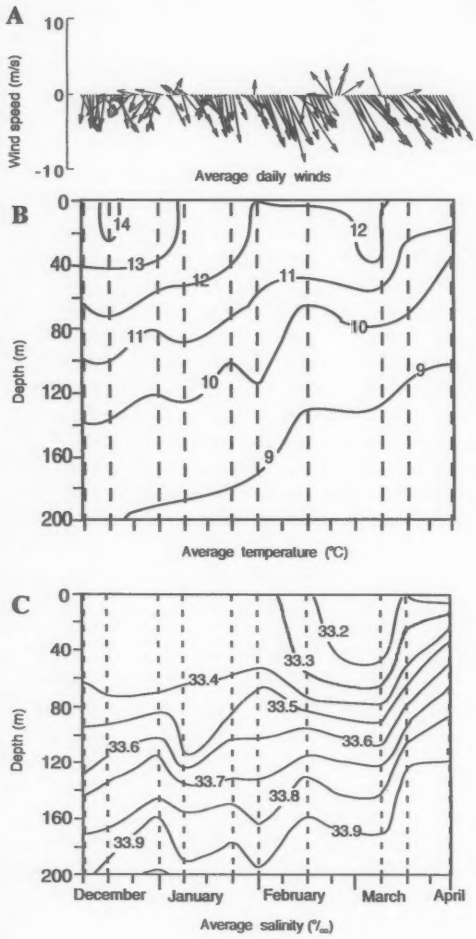

Figure 2

Wind, temperature, and salinity profiles for offshore Monterey Bay, California. (**A**) Wind vectors from December to April, as estimated from daily wind components measured at buoy 46042 and averaged from 1988 to 1991 (arrows point in the direction to which wind was blowing [north is toward top of page]); (**B**) weekly average temperature (°C); and (**C**) salinity (‰) in upper 200 m in the outer part of Monterey Bay during December to April, 1989–91. Weeks of CTD sampling are indicated with dashes. (Raw data from Rosenfeld et al., 1994b.)

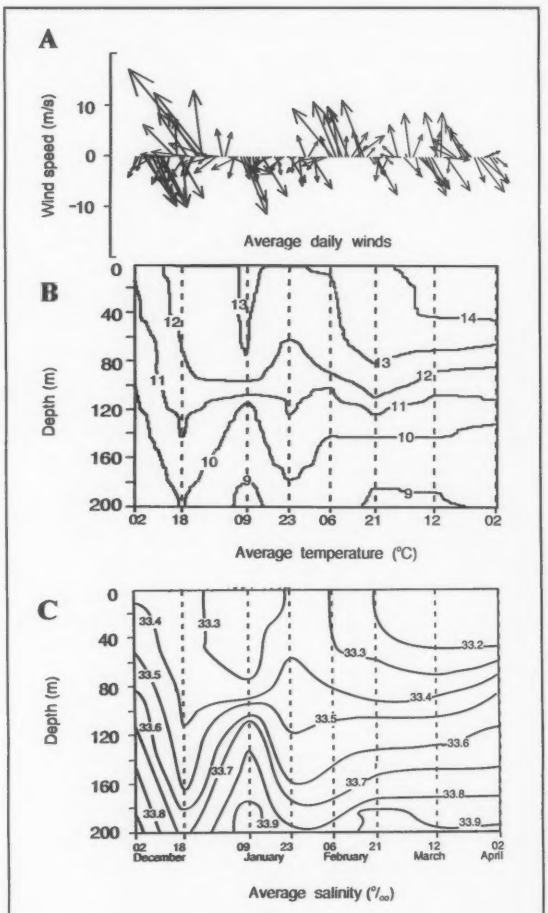

Figure 3

Wind, temperature, and salinity profiles for offshore Davenport, California. (**A**) Daily averaged wind vectors measured at buoy 46042 in Monterey Bay (arrows point in direction to which wind was blowing [north is toward top of page]); (**B**) temperature (°C); and (**C**) salinity (‰) in upper 200 m at an offshore station (19 km) during ichthyoplankton surveys 2 December 1991–2 April 1992. CTD sampling dates are indicated with dashes.

During winter 1993, a lens of warm surface water deepened from late January to mid-February, with 13.5°C water at 60 m along the transect line (Fig. 4B). Winds were variable, with no distinct periods of reversal. Unlike 1992, however, persistent wind from the northwest (favorable to upwelling) commenced in early March 1993 (Fig. 5A) and resulted in cooler water temperatures in the upper 80 m off Davenport by early April (Fig. 5B). This was the first evidence of upwelling during either year of the ichthyoplankton surveys, as indicated by the 10°C isotherm sloping up toward the coast from 19 km offshore in the 6 April 1993 CTD profile series (Fig. 4B).

Ichthyoplankton surveys

Patterns of distribution and abundance The 130 bongo-net tows made during ten ichthyoplankton surveys in 1991–92 (Table 1) contained 9,389 rockfish larvae; 39 tows made during four surveys in 1993 included 3,492 rockfish larvae. Rockfish larvae were collected during all surveys, occurring in 78.7% of all tows and in 100% of the tows made at the three stations 7–19 km from shore. Forty-seven percent of the rockfish larvae collected in 1992 and 66% in 1993 were identified as eight species or species-groups (Table 2). Shortbelly rockfish were numerically dominant both years, representing 46% of the total catch in 1993 and 29% in 1992. Shortbelly rockfish larvae occurred from late December to early May, largely in the offshore samples (13 and 19 km). Although much less numerous than shortbelly rockfish, blue, stripetail, and squarespot rockfish larvae also were relatively abundant each year (3–6% of the total). Although members of the "copper complex +" represented only 1–2% of the total catch and generally occurred in greater numbers offshore, they were the most abundant rockfish taxon identified at inshore stations (1 and 3 km).

Abundance of rockfish larvae varied among sampling dates and locations in 1991–92, with significant interaction between the two factors (ANOVA, $P<0.001$; Fig. 6A). Larvae were relatively abundant from January to April. Pairwise comparisons indicated that the large catches in early February 1992 at all stations were unique among all other time periods and that abundances across all stations early in the season (December and early January) were not significantly different from those that followed later (late-February, March, and April). Pairwise comparison of interstation abundance indicated two groups, one of stations closest to shore (1, 3, and 7 km) and another of the two offshore stations (13 and 19 km). The offshore stations had significantly greater abundance through time than did those inshore and, while abundance at most stations generally declined from a peak in early February, numbers of larvae remained relatively high through April at stations farthest from shore (13 and 19 km).

As with the 1991–92 collections, larval rockfish abundance varied significantly among sampling dates in 1993, with greatest abundances in February (Fig. 6B). Average abundances of larval rockfishes estimated at comparable stations and times from January through April were not significantly different between years (mean=602 larvae/10 m^2, SE=161 in 1992; mean=376 larvae/10 m^2, SE=179 in 1993; t-test, $P>0.383$), but distribution patterns differed. In contrast to the previous year, large catches of rockfish larvae occurred only at the two offshore stations in 1993. Significantly greater numbers of larvae occurred at the three stations closest to shore (1, 3, and 7 km) during January and February 1992, compared with the same months in 1993 (Kolmogorov-Smirnov tests, $P<0.05$).

Size, age, and birthdate distributions Size of larval shortbelly rockfishes collected on the same days in 1992 varied significantly among the 7, 13, and 19 km stations (ANOVA, $P<0.001$). Virtually all shortbelly rockfish larvae collected at the 7 km station were greater than 5 mm SL and significantly larger than those at the two offshore stations (Table 3). Shortbelly rockfish larvae were collected at the 7 km station only from early January to mid-March, and size composition remained similar throughout this period (overall mean=6.5 mm SL, SE=0.1). Size composition of shortbelly rockfishes did not differ significantly between the two offshore stations (overall mean=5.3 mm SL, SE=0.04), and the smallest larvae (<5 mm SL) were relatively abundant in all samples through early April.

Fewer samples and larvae collected at onshore stations in 1993 precluded among-station comparisons, although size composition of shortbelly rockfishes at the two offshore stations differed significantly (e.g. smaller larvae at the 13 km station compared with the 19 km station). The smallest larvae (<5 mm SL) were most abundant at the 13 km station in February and at the 19 km station in early April (Table 3).

Ages of 302 larval shortbelly rockfish collected in January–May 1992 and February–April 1993 were 1–28 d (Table 4). A least-squares linear model, $Length = a + b\,(Age)$, was fitted to separate sets of age-length data for each month in both years. Because no significant differences in growth rate were found among months (ANCOVA, $P>0.64$ [1992]; $P>0.73$ [1993]), age-length data were combined for each year. Moreover, there was no interannual difference in growth rate (ANCOVA, $P>0.90$). A least-squares linear model

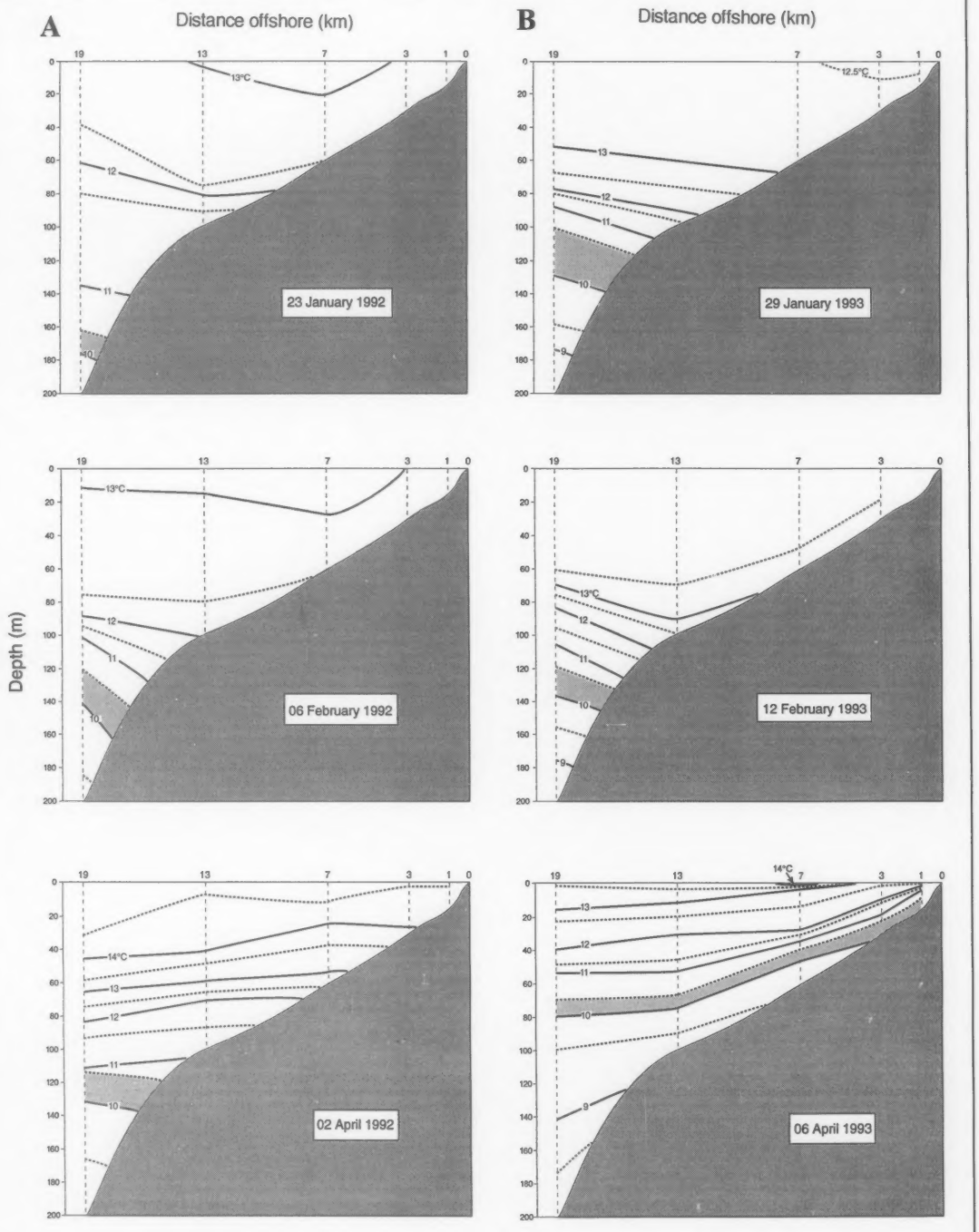

Figure 4

Vertical temperature profiles along the ichthyoplankton sampling transect off Davenport, California, during January, February, April, (**A**) 1992 and (**B**) 1993. The five CTD stations are indicated by distance offshore. Temperatures from 10.0 to 10.5°C are shaded for comparative purposes.

was computed for pooled age-length data because of the narrow age range (i.e. *Length*=4.63 + 0.20 [*Age*]; r^2=0.83; n=288). As an aside, the larval length at time of extrusion estimated by this model was 4.63 mm, which closely approximates the mean size of full-term shortbelly rockfish larvae collected from females off central California (4.7 mm SL; Laidig et al., 1991).

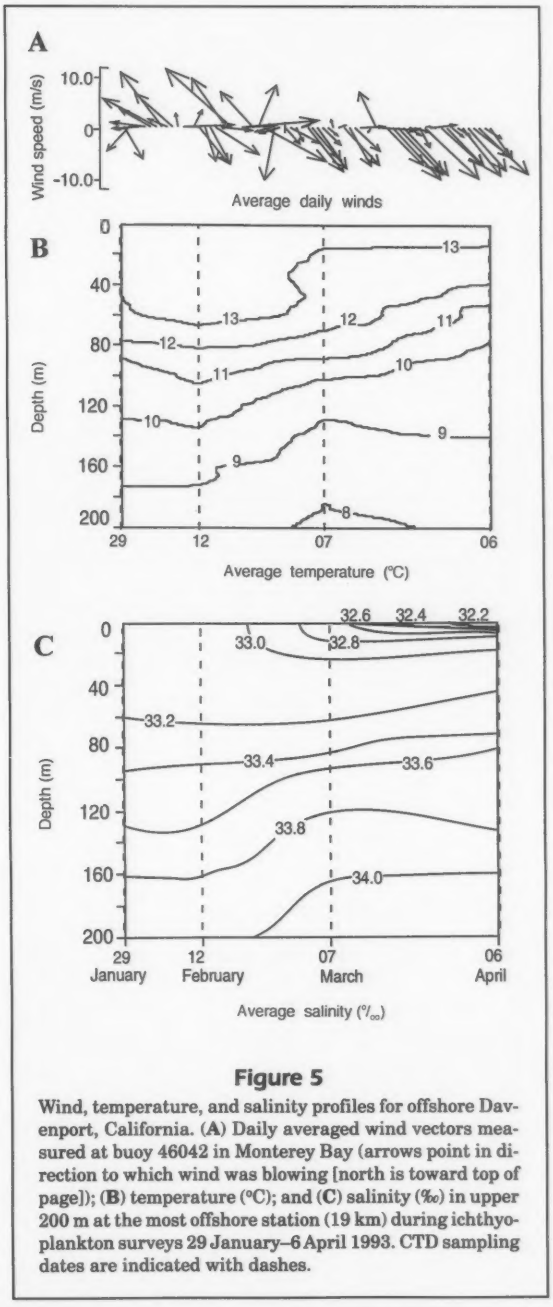

Figure 5

Wind, temperature, and salinity profiles for offshore Davenport, California. (**A**) Daily averaged wind vectors measured at buoy 46042 in Monterey Bay (arrows point in direction to which wind was blowing [north is toward top of page]); (**B**) temperature (°C); and (**C**) salinity (‰) in upper 200 m at the most offshore station (19 km) during ichthyoplankton surveys 29 January–6 April 1993. CTD sampling dates are indicated with dashes.

Birthdate distributions were compared between shortbelly rockfish larvae collected early in the season and pelagic juveniles collected from May to July. According to larval ages and collection dates, birthdates of shortbelly rockfishes extended from December to early May (median=5 February) 1992, and January to early April (median=12 February) 1993 (Fig. 7). Birthdates estimated from juvenile shortbelly rockfishes occurred much later in both years (Fig. 7). The relatively few pelagic juveniles (2.3 fish/trawl, n=56 midwater trawls; see Loeb et al.[1] for survey results) collected in May–July 1992 had an extremely narrow range of birthdates from 8 April to 2 May (median=21 April). Greater numbers of surviving juvenile shortbelly rockfishes during May–July 1993 (75.1 fish/trawl, n=64 midwater trawls; see Loeb et al.[1] for survey results) had a broader range of birthdates from 24 January to 7 June (median=15 March).

Larval blue rockfish, the second most abundant of the identified species, had a much narrower range of lengths (2.8–6.9 mm SL) and, unlike shortbelly rockfish, were abundant only from late January to early February in both years (Table 3). Size of larval blue rockfishes, collected on the same days in 1992, varied significantly among the 7, 13, and 19 km stations (ANOVA, P<0.001), with larger larvae occurring at the innermost station (mean size=5.0 mm SL, SE=0.1; Table 3). As with shortbelly rockfish larvae, size composition of blue rockfishes was not significantly different between the two offshore stations (overall mean=4.5 mm SL, SE=0.1). Although 1993 collections were limited and comparisons not statistically significant, there was a continued trend of smaller blue rockfish larvae farther offshore.

Ages of 96 larval blue rockfish collected in January–February of 1992 and 1993 ranged from 2 to 21 d (Table 4); only 7 of these specimens were from 1993 because of problems with preservation. Because growth rates estimated over similar age ranges were not significantly different in January and February 1992 (ANCOVA, P>0.78), age-length data were combined and a least-squares linear model was calculated (i.e. *Length*=3.98 + 0.14 [*Age*]; r^2= 0.63; n=96). Birthdates were estimated for all blue rockfish larvae collected in 1992 and 1993 by using fish length and this growth model. Birthdate distribution was narrow in both years, ranging from 31 December 1991 to 21 February 1992 and from 12 January to 12 February 1993; the median birthdate was 27 January in both years. Birthdates could not be compared with those of pelagic juvenile blue rockfishes because no juveniles were collected in 56 midwater trawl

Table 2

Standardized abundance (number per 10 m^2) of larval rockfishes in bongo-net tows collected off Davenport, California, December 1991–June 1992 and January–April 1993. "—" indicates that zero larvae were collected.

	2 Dec					18 Dec					9 Jan					23 Jan					6 Feb				
	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19
1991–1992																									
S. jordani	—	—	—	—	—	—	—	—	4	8	—	—	34	29	186	4	—	144	269	21	—	—	152	656	166
S. mystinus	—	—	—	—	—	—	3	—	—	—	—	7	15	—	38	2	4	85	21	109	—	—	109	180	90
S. hopkinsi (?)	—	—	—	—	—	—	3	12	12	—	—	—	49	4	34	—	—	25	25	11	—	—	67	46	54
S. saxicola	—	—	—	—	—	—	—	—	—	4	—	—	4	—	17	—	—	11	17	189	—	—	4	8	54
Copper complex +	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	7	—	4	3	4	38	17	27
S. paucispinis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	—	—	21	64	32	—	—	4	8	18
Sebastosomus +	—	—	—	—	—	—	—	8	—	—	—	—	4	—	—	—	—	—	—	4	—	—	42	—	36
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	—
Unidentified	—	3	—	13	37	4	8	19	56	62	—	3	42	69	169	8	4	113	191	186	3	61	160	3,127	714
Damaged	—	—	—	3	—	—	—	4	—	—	—	—	4	—	47	—	—	18	7	21	—	4	29	75	81
All *Sebastes* spp.	—	3	—	16	37	4	14	47	71	74	—	10	151	101	512	14	8	423	593	575	6	69	610	4,122	1,239

	21 Feb					12 Mar					2 Apr					4 May		16 Jun					
	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	13	19	3	7	13	Stand. abun.	Overall % abun.	Count (N)
1992 (cont'd)																							
S. jordani	—	—	43	131	—	—	4	41	380	823	—	—	—	—	372	49	3	—	—	—	3,520	29	836
S. mystinus	—	—	9	26	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	719	6	183
S. hopkinsi (?)	—	—	43	33	18	—	—	4	23	14	—	—	—	—	4	4	3	—	—	—	487	4	121
S. saxicola	—	4	—	23	4	—	—	—	14	29	—	—	—	19	—	—	—	—	—	—	401	3	104
Copper complex +	—	—	17	3	4	8	4	8	—	—	6	7	4	27	—	—	—	—	10	4	207	2	52
S. paucispinis	—	—	—	3	13	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	189	2	50
Sebastosomus +	—	—	—	3	4	—	—	—	—	—	—	—	—	—	4	—	—	—	—	4	109	1	26
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	12	0.1	3
Unidentified	—	12	72	311	88	—	—	4	135	91	—	—	4	22	29	185	128	—	—	4	6,137	50	1,526
Damaged	—	—	26	7	9	—	—	4	28	29	—	—	—	—	—	—	—	—	—	—	394	3	94
All *Sebastes* spp.	—	16	208	540	162	8	8	62	585	987	6	7	7	68	410	238	138	—	10	12	12,175	100	2,995

	29 Jan					12 Feb			7 Mar		6 Apr					
	1	3	7	13	19	7	13	19	3	19	3	13	19	Stand. abun.	Overall % abun.	Count (N)
1993																
S. jordani	—	—	21	153	189	2	1,274	92	—	274	—	44	199	2,248	46	534
S. saxicola	—	—	—	32	76	—	91	70	—	9	—	—	4	282	6	62
S. mystinus	—	—	5	90	167	—	25	15	—	—	—	—	—	302	6	58
S. hopkinsi (?)	—	—	11	11	—	—	147	44	11	—	—	—	—	224	5	49
Sebastosomus +	—	—	—	48	11	—	45	19	—	7	—	—	—	130	3	28
Copper complex +	—	—	5	—	—	—	35	15	—	2	—	—	—	57	1	13
S. paucispinis	—	—	—	11	5	—	—	11	—	—	—	—	4	31	1	7
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	—	8	53	99	156	25	395	282	—	126	—	39	188	1,371	28	343
Damaged	—	—	11	37	—	—	243	—	—	—	—	—	—	291	6	57
All *Sebastes* spp.	—	8	106	480	604	27	2,255	549	11	418	—	83	393	4,936	100	1,151

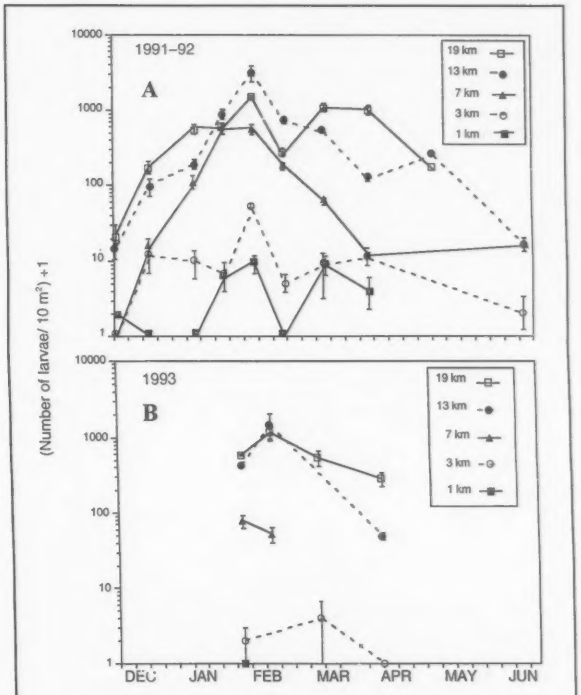

Figure 6

Larval rockfish abundance (per 10 m^2) at five stations along an onshore–offshore transect, Davenport, California. Each point is the average of 3 replicates, except for 2 tows made at the 7 km station on 2 December 1991 and single tows made at two offshore stations in May 1992; error bars = 1 SE. (**A**) 2 December 1991–16 June 1992; (**B**) 29 January–6 April 1993.

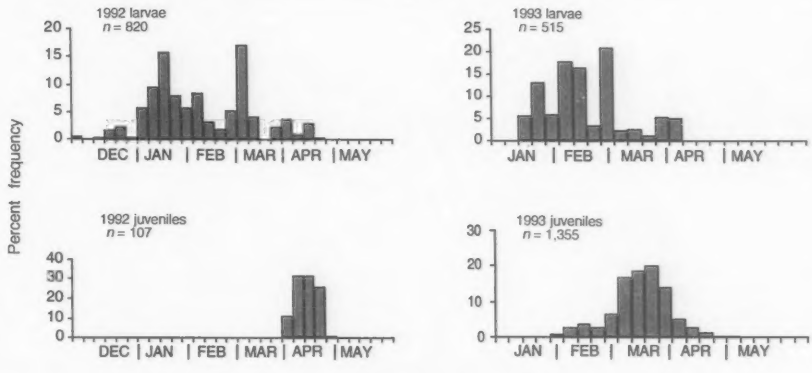

Figure 7

Hatch date distributions for shortbelly rockfish, *Sebastes jordani*, estimated from age of larvae collected January–April 1992 and 1993 and from age of juveniles collected June 1992 and May–July 1993.

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Table 3

Size (mean, SE, and *n*) of larval shortbelly and blue rockfish collected by standard oblique bongo-net tows at stations 7, 13, and 19 km off Davenport, California, December 1991–April 1993.

	1991–92									1993				
	18 Dec	9 Jan	23 Jan	6 Feb	21 Feb	12 Mar	2 Apr	4 May	Overall	29 Jan	12 Feb	7 Mar	6 Apr	Overall
Shortbelly rockfish														
7 km mean (mm)	—	6.6	6.3	6.7	6.2	6.1	—	—	6.5	4.8	6.3	—	—	5.1
SE	—	0.2	0.1	0.2	0.4	0.2	—	—	0.1	0.1	—	—	—	0.3
n	0	9	41	36	10	10	0	—	106	4	1	—	—	5
13 km mean (mm)	6.1	4.8	6.0	4.8	5.2	6.0	—	7.5	5.4	5.1	4.9	—	6.2	4.9
SE	—	0.1	0.1	0.1	0.1	0.1	—	0.4	0.1	0.1	0.1	—	0.4	0.1
n	1	8	77	155	39	82	0	11	373	31	233	—	9	273
19 km mean (mm)	7.0	5.6	5.5	5.0	—	5.0	4.7	6.5	5.0	5.6	6.3	5.8	5.3	5.7
SE	1.3	0.1	0.3	0.2	—	0.1	0.1	—	0.1	0.1	0.3	0.1	0.1	0.1
n	2	44	6	35	0	166	84	1	338	37	24	121	55	237
Blue rockfish														
7 km mean (mm)	5.8	5.0	4.8	5.3	5.4	—	—	—	5.0	4.1	—	—	—	4.1
SE	—	0.2	0.1	0.1	0.5	—	—	—	0.1	—	—	—	—	—
n	1	4	24	25	2	0	0	0	56	1	0	0	0	1
13 km mean (mm)	—	—	4.0	4.4	4.5	—	—	—	4.4	4.4	4.6	—	—	4.4
SE	—	—	0.2	0.1	0.1	—	—	—	0.1	0.1	0.2	—	—	0.1
n	0	0	6	43	7	0	0	0	56	19	5	0	0	24
19 km mean (mm)	—	4.7	4.4	4.9	4.3	—	—	—	4.6	4.2	4.4	—	—	4.2
SE	—	0.2	0.1	0.2	0.3	—	—	—	0.1	0.1	0.2	—	—	0.1
n	0	9	31	20	5	0	0	0	65	33	4	0	0	37

samples from May to July 1992 and only 29 individuals (0.5% of total catch) occurred in 65 midwater trawl samples from May to July 1993 (Loeb et al.[1]).

Discussion

Larval rockfish are a dominant group in the ichthyoplankton along the west coast of the United States, with relatively high abundances occurring seasonally in surveys off southern and central California (Barnett et al., 1984, Moser and Boehlert, 1991) and off northern California, Oregon, and Washington (Richardson and Pearcy, 1977; Richardson et al., 1980; Boehlert et al., 1985; Doyle et al., 1993). During our study, mean overall abundance of larval rockfish ranked second only to that of the northern anchovy (*Engraulis mordax*; 749 larvae/10 m^2) in 1992 and Pacific hake (*Merluccius productus*; 1,520 larvae/10 m^2) in 1993 (B. Daly, unpubl. data). Larval rockfishes are generally characterized as members of offshore assemblages; their abundance increased with distance from shore in our study as well as in the surveys cited above. Distribution of at least the youngest larvae is defined by the location of spawning adults, which for many rockfish species is principally over rock bottom along the edge of the continental shelf and submarine canyons. This is supported by the significantly greater numbers of small shortbelly rockfish larvae in samples collected at our most offshore station, located over Año Nuevo submarine canyon.

Declines in somatic and reproductive condition (VenTresca et al., 1995) and decreased fat storage (Lenarz and Wyllie Echeverria, 1986) in adult rockfish collected off central California during El Niño years likely are responses to reduction in primary prey biomass. Mullin and Conversi (1989) documented large-scale reductions in abundance of euphausiids and smaller zooplankton (e.g. the pri-

Table 4

Size, age, and number of larval shortbelly, *Sebastes jordani*, and blue, *S. mystinus*, rockfish included in age and growth estimates in 1992 and 1993.

	1992						1993				
	Jan	Feb	Mar	Apr	May	Overall	Jan	Feb	Mar	Apr	Overall
Shortbelly rockfish											
No. aged	54	60	34	15	12	175		47	36	44	127
Mean age (d)	8.4	8.2	6.3	2.6	11.6	7.6		6.7	7.2	4.5	6.1
SE	0.8	0.9	0.7	0.7	1.3	0.5		0.8	0.7	0.7	0.4
Range (d)	1–28	1–28	1–20	1–11	4–18	1–28		1–21	2–22	1–21	1–22
Mean SL (mm)	6.3	6.2	5.9	5.2	7.4	6.2		5.8	6.1	5.8	5.9
SE	0.2	0.2	0.2	0.2	0.4	0.1		0.2	0.2	0.2	0.1
Range (mm)	4.0–10.8	3.9–9.8	4.2–8.8	4.3–6.3	5.0–9.7	3.9–10.8		4.3–9.0	4.8–9.0	4.2–9.2	4.2–9.2
Blue rockfish											
No. aged	43	46				89	3	4			7
Mean age (d)	4.3	6.3				5.3	8.0	6.0			6.9
SE	0.3	0.7				0.4	4.0	1.6			1.8
Range (d)	2–14	2–21				2–21	4–16	2–10			2–16
Mean SL (mm)	4.7	4.8				4.8	5.1	4.5			4.8
SE	0.1	0.1				0.1	0.4	0.2			0.2
Range (mm)	3.4–6.1	2.8–6.9				2.8–6.9	4.4–5.9	4.0–5.0			4.0–5.9

mary prey of juvenile and adult rockfishes) during the 1958 El Niño. Poor condition of adult rockfishes could influence larval production and reproductive timing. Abundance of rockfish larvae in our study, however, was not significantly different between the two years of the extended El Niño event along the central California coast and was much greater than estimates from earlier ichthyoplankton surveys coastwide. Greatest mean abundance of rockfish off Oregon was 350 larvae/10 m^2 in May 1971 (Richardson and Pearcy, 1977), 199/10 m^2 in March 1972, and 176/10 m^2 in March 1973 (Richardson et al., 1980). Peak abundance of rockfish sampled during CalCOFI surveys in February 1951–81 averaged about 200 larvae/10 m^2 off northern and central California and 90 larvae/10 m^2 off southern California (Moser and Boehlert, 1991). Average larval rockfish abundance estimated from those CalCOFI lines (i.e. 63, 67, 70) and stations (i.e. 49–57) closest to our sampling sites was 486 larvae/10 m^2 in February, 1960–84. We estimated a mean abundance of 990 rockfish larvae/10 m^2 at the three offshore stations in February during our 2-year survey. This figure demonstrates that overall larval abundance was not negatively affected by an El Niño event and that the area north of Monterey Bay is a significant production ground for larval rockfishes. This finding is substantiated by the results of pelagic juvenile rockfish surveys along California, which indicate a center of distribution in this area (Larson et al., 1994).

Further, the El Niño event of 1991–93 did not seem to have caused a significant shift in overall timing of parturition, at least for the two species that dominated our ichthyoplankton surveys. Median hatch dates of shortbelly rockfish larvae collected during late winter and early spring of 1991–92 and 1993 were similar to each other (first and second week in February, respectively), and to the primary month of parturition (i.e. February) according to reproductive stages of this species off central California from 1977 to 1984 (Wyllie Echeverria, 1987). Release of blue rockfish larvae during our study likewise was as expected (i.e. January; Wyllie Echeverria, 1987). Absence of sampling in late December 1992 could have masked an unlikely peak of parturition earlier in the 1993 season.

Although reproductive timing and production seemingly were not influenced by the prolonged El Niño event, occurrence of juvenile rockfishes in trawl samples collected in late spring and summer was dramatically different between years. Extremely low numbers of pelagic juvenile rockfish were encountered during midwater trawl surveys (n=56 trawls) conducted from 4 May to 10 July 1992 north and south of Monterey Bay (Loeb et al.[1]). In contrast, pelagic juvenile rockfishes collected during the same time period in 1993 (n=65 trawls) were 20 times more abundant, comprised twice as many taxa, and were substantially larger than juveniles collected in 1992 (Loeb et al.[1]). Shortbelly, copper-complex, and kelp rockfishes dominated the relatively low numbers of

rockfish juveniles in 1992. The 1993 pelagic juveniles were dominated by shortbelly, squarespot, halfbanded (*S. semicinctus*), and chilipepper (*S. goodei*) rockfishes, in that order. All of these species can produce larvae relatively late in the season.

Among the dominant species, only those shortbelly rockfish larvae released late in the season (March and April) were represented in the birthdate distributions of juveniles collected in the summer of both years of the El Niño. The few pelagic juvenile shortbelly rockfishes collected in May–June during the 1983 El Niño event also had late birthdates (Woodbury and Ralston, 1991). It is clear that the largest proportion of larval shortbelly rockfish production, >65% occurring prior to March during both years of the 1991–93 El Niño event, did not survive until the juvenile surveys conducted during the summers of 1992 and 1993. Blue rockfishes, largely produced in January and February and ranked second (1992) and third (1993) in larval catches, were not collected at all during pelagic juvenile surveys in May–July 1992 (56 midwater trawls; Loeb et al.[1]), and represented 0.5% (n=29 individuals) of the total catch of pelagic juveniles in May–July 1993 (65 midwater trawls; Loeb et al.[1]). Stripetail rockfish, another species whose parturition period is restricted to early in the year off central California (i.e. November–March with a peak in January [Wyllie Echeverria, 1987]), was relatively abundant in the plankton both years but rare in the pelagic juvenile collections (<0.1 and 0.5 fish per trawl).

In accordance with the results of the surveys by Loeb et al.,[1] subtidal observations along the central coast made by California's Department of Fish and Game Sportfish Project biologists indicated that few juveniles of nearshore rockfish species recruited to rocky and kelp canopy areas off the Monterey Peninsula during May–August 1992 (VenTresca[3]). Low abundance of pelagic juvenile rockfishes off central California also was noted during May–June 1992 surveys conducted by scientists of the NMFS Tiburon Laboratory (Lenarz et al., 1995; Ralston and Howard, 1995) and during previous El Niño events of 1983 and 1986 (Wyllie Echeverria et al., 1990). In contrast, overall abundance of pelagic juvenile rockfishes in 1993 was fourth greatest among the past eight years of NMFS-Tiburon surveys (Lenarz et al., 1995), and relatively high numbers, dominated by blue rockfishes, settled off Monterey during June–September 1993 (VenTresca[3]). Substantially greater abundance and larger sizes of pelagic juvenile rockfishes during May–July 1993 indicated that recruitment was likely related to the timing of optimal environmental conditions during larval development. This is consistent with the dome-shaped relationship described by Ralston and Howard (1995) between interannual variability in winter SST's and estimates of year-class strength for blue and yellowtail rockfishes off central California collected from 1983 to 1992 (e.g. juvenile abundance was lowest when SST's were either exceptionally low or high during winter months of larval production).

Mortality of fishes during the larval stage has been attributed to starvation and predation; debate continues as to which factor is more significant for successful recruitment (Hunter, 1981; Bailey and Houde, 1989). There was no evidence from our ichthyoplankton samples that suggested that young rockfishes were starving in either year of the El Niño event. Growth of young shortbelly rockfishes was similar throughout the parturition period, no differences were detected between the two years, and growth in 1992–93 was similar to that estimated for this species from the central California during non-El Niño years (i.e. in 1989 [Laidig et al., 1991] and in 1991 [Ralston et al., 1996]). Moreover, blue rockfish, although relatively common in the ichthyoplankton, abruptly disappeared at young ages (i.e. when many were still dependent on yolk reserves) from samples collected in late January and early February and had very poor recruitment to the pelagic juvenile stage in 1992. This finding suggests acute mortality, perhaps coincident with onshore transport and increased encounter rates with predators.

Time of release of rockfish larvae can contribute to variation in year-class abundance by influencing the spatial and temporal coincidence of larvae, prey availability, predator abundance, and favorable environmental conditions, such as temperature, upwelling, and transport (Parrish et al., 1981; Methot, 1983; Checkley et al., 1988; Nyman and Conover, 1988). Rockfish larvae were more abundant and the dominant species (shortbelly rockfish) was significantly larger at onshore stations in 1992 than in 1993, indicating retention of larvae nearshore during the first year of the El Niño event. These occurrences coincided with onshore advection of water, as characterized by reversals in wind direction and by warmer, less saline water that occurred during peak larval rockfish abundance in February 1992.

Larval retention in nearshore areas could be responsible for heavy mortality, possibly through increased predation. Significant changes in zooplankton assemblages associated with wind relaxation and subsequent onshore transport have been noted along central California (Farrell et al., 1991), and abun-

[3] VenTresca, D. 1995. California Department of Fish and Game, 20 Lower Ragsdale Dr., No. 100, Monterey, CA 93940. Unpubl. data.

dance of several potential larval fish predators can increase nearshore during these events. During the 1958 El Niño event, the California Current moved shoreward, and abundance of potential larval fish predators (siphonophores and chaetognaths) increased in inshore coastal waters (Smith, 1985). Mean zooplankton biomass, dominated by copepods, euphausiids, and chaetognaths, was significantly greater in nearshore than in offshore areas of Monterey Bay during the first year of the 1991–93 El Niño event (Baduini, 1995); this trend reversed after upwelling commenced in early April 1993. Limited information on chaetognaths (largely *Sagitta bipunctata*) collected in our ichthyoplankton samples (Bridges[4]) indicated extremely high numbers (e.g. up to 20,000 individuals/10 m^2 at 3 km from shore, which represented five times the greatest larval rockfish abundance) in early February 1992, coincident with the wind reversal, onshore transport of water, and peak abundance of larval rockfish. At least 20% of these animals were >11 mm in length, a size at which chaetognaths are capable of ingesting a larval fish (senior author, unpubl. data). The lack of upwelling and associated offshore transport during subsequent months could prolong nearshore retention and further reduce recruitment success.

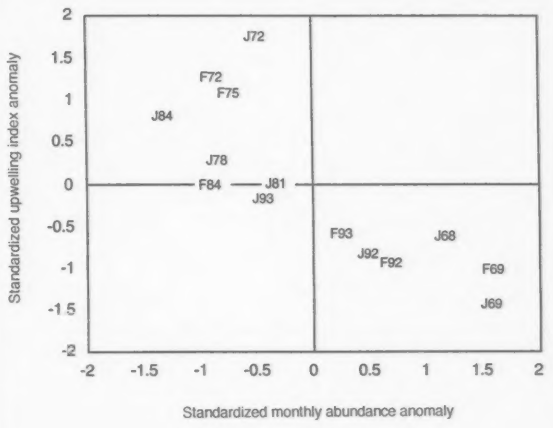

Figure 8

Comparison of mean monthly standardized anomalies of larval rockfish abundance in January (J) and February (F) of various years (indicated by last two digits of each year), with those of upwelling indices estimated at 36° and 39°N and averaged over a 4-day period prior to and including day of ichthyoplankton sampling. Estimates of larval abundance prior to our study are from CalCOFI ichthyoplankton surveys conducted inshore of station 60 along lines 63, 67, and 70 (Moser et al., 1993). Standardized anomalies were calculated by using data from our study and the CalCOFI surveys.

Although predation on fish eggs and larvae has been generally characterized as a density-independent control on fish populations (Bailey and Houde, 1989), exceptions include co-occurrence of predators and prey concentrated in small areas (e.g. high density of herring larvae and scyphomedusae [Moller, 1984]) and prey-switching when preferred diet is not available (Pepin, 1987). Although small copepods are the preferred prey of larval fish and many of their invertebrate predators, reduction in this food source during El Niños (McGowan, 1985; Miller et al., 1985) could increase the likelihood of predation on small fish larvae. Several species of chaetognaths prey secondarily on young fish larvae (Kuhlmann, 1977), and an inverse relationship between larval fish abundance and chaetognath densities has been described from CalCOFI samples collected during the 1958 El Niño off California (Alvariño, 1980).

In contrast, increased upwelling intensity and offshore transport during March and April 1993 may have facilitated survival of larval stages for those species with broad periods of parturition by advecting them from nearshore areas. Although there is a significantly negative relationship (r^2=0.63; P<0.001) between larval rockfish abundance and offshore Ekman transport (i.e. positive upwelling indices) during peak production in January and February (Fig. 8), dispersal mechanisms like upwelling seem to be important in determining recruitment to the juvenile stage (Ralston and Howard, 1995). Breaker (1983) characterized the spring transition from winter ocean conditions to the onset of upwelling and offshore Ekman transport as an abrupt decrease in SST (e.g. 0.38–0.59°C per day) off central California (36°26'N); dramatic spring transitions occurred in six of the twelve years (1971–83), with suppression of transition during El Niño events. According to examinations of daily SST's from the same station during the 1991–93 El Niño event (Schwing[5]), a spring transition did not occur at all in 1992 and a modest transition (0.34°C per day) was initiated in early April 1993, coinciding with the birthdate distribution of the surviving cohort of shortbelly rockfish juveniles.

In conclusion, the extended El Niño event of 1991–93 provided a unique opportunity to assess abundance and distribution of larval rockfishes during a

[4] Bridges, J. 1994. Department of Biology, University of California, Santa Cruz, CA 95064. Unpubl. data.

[5] Schwing, F. 1995. Pacific Fisheries Environmental Group, Natl. Mar. Fish. Serv., Pacific Grove, CA. Unpubl. data.

significant environmental perturbation, an opportunity that yielded some insight into the recruitment process. Characterizing the link between larval rockfish distribution and the hydrographically dynamic environment of the central California coast required finer-scale spatial and temporal sampling than has been achieved previously. Rockfish larvae were more abundant and larger at onshore stations in 1992, coinciding with onshore advection of water during the onset of the El Niño event and suggesting retention of larvae nearshore; abundance of juvenile rockfishes in nearshore areas later in that year was extremely low. Initiation of upwelling in March and April of 1993 and the occurrence of fewer rockfish larvae at onshore stations suggest greater offshore transport during the second year; juvenile rockfish abundance was greater than the previous summer. From these data, we suggest that substantially higher survival and recruitment of juvenile rockfishes in 1993 likely are due to increased offshore transport and dispersal, and possibly lower predation, during the larval stages.

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Do herring grow faster than orange roughy?

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In growth studies it is common to find the statement "P grows faster than Q". However, it is much less common to find a clear definition of what the author means by that statement. What is it about two sets of growth parameters, or two growth curves, that should make us conclude that "P grows faster than Q"? In this note I will show that this is not as simple a question as it may seem. There are several plausible ways of answering it and these have very different consequences. Thus, the statement "P grows faster than Q" is ambiguous and it is important for authors to be specific about what they mean by it. I will also give reasons for preferring one of the possible meanings.

In what follows it will sometimes be convenient to refer to the two entities being compared as "species P" and "species Q." However, my conclusions are the same whether the growth comparison is made within species (e.g. males vs. females [Horn, 1993; Hostetter and Munroe, 1993; Kitagawa et al., 1994; Collins et al., 1995], one time period vs. another [Raspopov, 1993; Collins et al., 1995], or one area vs. another [Horn, 1993; Savard et al., 1994]), or between species (Arkhipkin and Nekludova, 1993; Gorny et al., 1993; Milton et al., 1993; Potts and Manooch, 1995).

Before proceeding, it is useful to restrict the scope of the question being considered. First, only the mean growth for a "species" is considered; therefore between-individual variability in growth is ignored. Second, I will assume that we have perfect knowledge about the growth of P and Q; i.e. statistical uncertainty is ignored. Third, I will consider only unqualified comparisons such as "P grows faster than Q," comparisons that apply only to a portion of the life history (e.g. "P grows faster than Q up to age 1") are excluded. The purpose of these restrictions is to allow for a simpler presentation. Without them, the picture is more complex, but the results given below will still apply, although not in precisely the same form.

Six methods of growth comparison

There are at least six plausible methods for comparing growth (Table 1). With method 1, we would say that P grows faster than Q if $L_{t,P} > L_{t,Q}$ for all t, where $L_{t,P}$ and $L_{t,Q}$ are the lengths at age t for species P and Q, respectively. The rationale behind this method is that $L_{t,P} > L_{t,Q}$ implies that P must have grown faster than Q (at least on average) over the period up to age t. Now, rather than comparing average growth rates over a period of time it may be more sensible to compare instantaneous growth rates. This is the reason for method 2. However, it may be argued that method 2 makes no sense when $L_{t,P}$ is very different from $L_{t,Q}$. For example, a growth rate of 10 cm/yr is fast for an animal of size 20 cm but slow for an animal of size 200 cm. There are two ways to deal with this difference: we can either insist that the comparison be made when the animals are of the same size (method 3), or we can standardize the growth rates by dividing by length (methods 4 and 5). (Method 5 is included here for completeness, but it is easy to show that it is exactly equivalent to method 3.) Method 6 could be appropriate where growth is asymptotic and the asymptotes for P and Q are different. Here the species that approaches its asymptote faster is said to grow faster. Of course, this method is not fully defined until we specify what we mean by "the rate at which the asymptote is approached."

To illustrate the difference between these methods we will assume that growth is adequately described by the von Bertalanffy equation with $t_0 = 0$, i.e.

$$L_t = L_\infty(1 - e^{-kt}).$$

Table 1

Six methods for comparing the mean growth of two species or populations. The absolute growth rate is the slope of the length-at-age curve (with dimension length/time) and the relative growth rate is this slope divided by the length (dimension 1/time).

Method 1:	compare lengths at each age
Method 2:	compare absolute growth rates at each age
Method 3:	compare absolute growth rates at each length
Method 4:	compare relative growth rates at each age
Method 5:	compare relative growth rates at each length
Method 6:	compare rates at which the asymptotic size is approached

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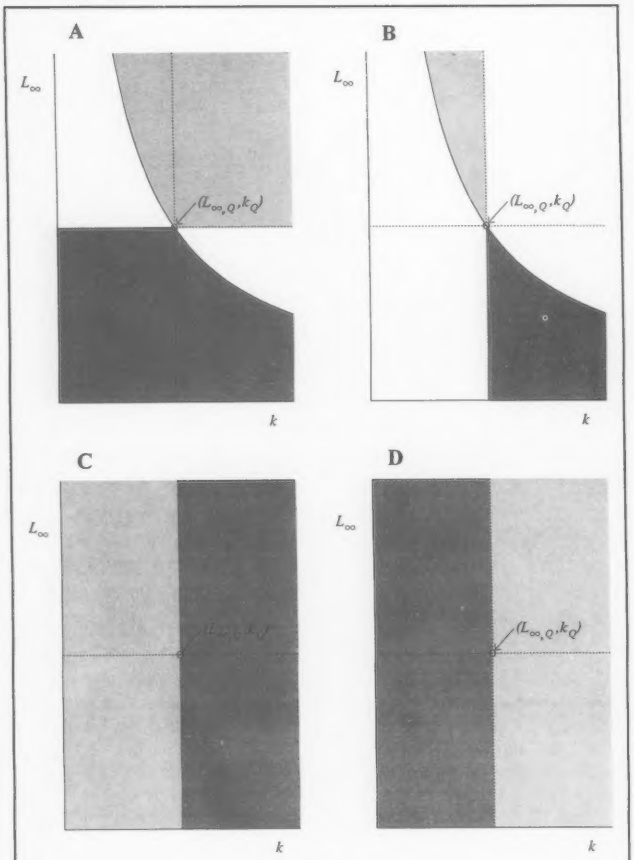

Figure 1

Illustration of the six methods of growth comparison in Table 1 when growth follows the von Bertalanffy equation. In each panel, the central point, 'o', represents the growth parameters for species Q, $(L_{\infty,Q},k_Q)$. Species P is said to grow faster (or slower) than species Q if the point $(L_{\infty,P},k_P)$ lies in the light (or dark) shaded area of the graph. In the unshaded areas, no comparison can be made over the whole life history (so P may be faster than Q at one age [or length] and slower at another). Comparisons are for (**A**) methods 1, 3, and 5; (**B**) method 2; (**C**) method 4; and (**D**) method 6. See Table 1 for definitions of methods. The curved line in panels A and B is $L_\infty = L_{\infty,Q}k_Q/k$. (Details of the derivation of this Figure are available from the author).

With this assumption, method 6 is fully defined because the parameter k determines the rate at which the asymptote is approached; the bigger k is, the faster the asymptote is approached. Thus, according to method 6, P grows faster than Q if $k_P > k_Q$.

Now, given growth parameters $L_{\infty,Q},k_Q$ for Q, we are in the position to address the question, "What range of values can $L_{\infty,P},k_P$ take if we are to say that P grows faster (or slower) than Q?". Figure 1 shows that the answer to this question depends strongly on which of the six methods of comparison is used. Methods 1, 2, and 5 give identical answers, but these are very different from the answers from the other methods. Methods 4 and 6 give completely opposite answers. For methods 4 and 6, we can always say either "P grows faster than Q" or "Q grows faster than P" (as long as the growth rates are not identical). However, for all other methods in Table 1, it will sometimes not be possible to make either of these statements without qualification. For example, in the unshaded areas of Figure 1A, P grows faster than Q at some ages (or lengths) and slower than Q at others (according to methods 1, 3, and 5).

Method 6: A comparison of rates at which the asymptotic size is approached

I suggest that method 6 is the most "natural" method of growth comparison, in the sense that it produces common-sense results. To see why, consider the question in the title of this paper. Orange roughy, *Hoplostethus atlanticus*, is described as "very slow-growing" (Fenton et al., 1991) and herring, *Clupea harengus*, is generally considered to be fast-growing; therefore the answer to this question should be "yes." Given growth parameters for orange roughy ($L_{\infty,Q}$=40 cm, k_Q=0.044/yr; Fenton et al., 1991) and any of the sets of herring parameters given by Pauly (1980) (range: $L_{\infty,P}$=19.4 – 36.0 cm, k_P = 0.21– 0.48/yr), the point $(L_{\infty,P},k_P)$ would lie in the right-hand unshaded space in Figure 1A (and in the corresponding position in the other panels of Figure 1). This means that with methods 1, 2, 3, and 5 there would be no clear-cut difference in growth rates between these species and that with method 4 herring would grow slower than orange roughy. Only method 6 reaches the common-sense conclusion.

Another reason to prefer method 6 is that it ignores asymptotic size (L_∞). It seems to me that comparisons of this parameter determine only whether one species is bigger than another, not whether growth is faster or slower. In other words L_∞ describes size, not growth rate. But note that, for the methods covered by Figure 1, A and B, P cannot be judged to grow faster than Q unless $L_{\infty,P} > L_{\infty,Q}$. This confusion between measures of size and growth rate is illustrated by Figure 2. Method 6 ranks curve P

as the slowest-growing because it is the slowest of the three in approaching its asymptote; with methods 1, 2, 3, and 5, the ranking is reversed because of the influence of L_∞ (it is also reversed for method 4, but not because of L_∞).

So far, method 6 has been defined only where growth follows the von Bertalanffy equation with $t_0 = 0$. This definition works equally well even if $t_0 \neq 0$ (this parameter simply determines the horizontal position of the growth curve and is therefore irrelevant in describing the speed of growth). The definition also extends naturally to the Gompertz and logistic growth equations as long as growth is considered only to the right of the inflection point. Both these equations have a rate parameter precisely analogous to k (this is the parameter g in equations 3 and 4 of Schnute, 1981). However, more complex growth models (e.g. the four-parameter model of Schnute, 1981) are so flexible that it seems difficult to rank growth curves along a single dimension, from slower to faster. A simple solution, which is consistent with method 6, would be to determine the age at which a species reaches 90%, say, of L_∞. The younger this is, the faster-growing is the species.

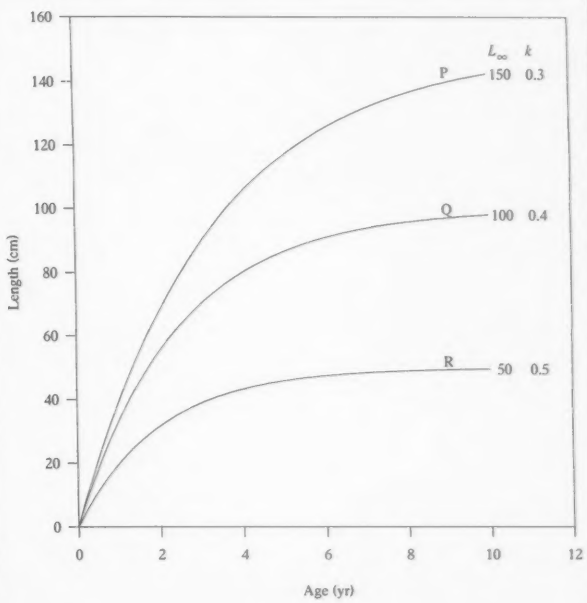

Figure 2

Example of three von Bertalanffy growth curves whose ranking, from slowest- to fastest-growth, is P, Q, and R for method 6 but the reverse for all other methods in Table 1.

Conclusions

The main conclusion of this paper is that statements like "P grows faster than Q" are ambiguous unless the method of growth comparison (e.g. one of the methods in Table 1) is specified. To some extent it does not matter which method is used as long as this is clearly stated. However, I have given some reasons to believe that method 6 is the most natural method. Amongst these reasons is the observation that, for von Bertalanffy growth, it is the parameter k that describes growth rate; L_∞ merely describes (eventual) size.

In order to make a point, the title of this paper refers to comparisons between disparate species. However, my main conclusion applies whether the growth comparison is made within or between species. I am happy to agree with an anonymous referee who asserted (forcefully) that some authors may not share my preference for method 6 (particularly for within-species comparisons).

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Announcement

The editorial staff of *Fishery Bulletin* would like to thank the following referees for their time and efforts in providing reviews of the manuscripts published in 1996. Their contributions have helped ensure the publication of quality science.

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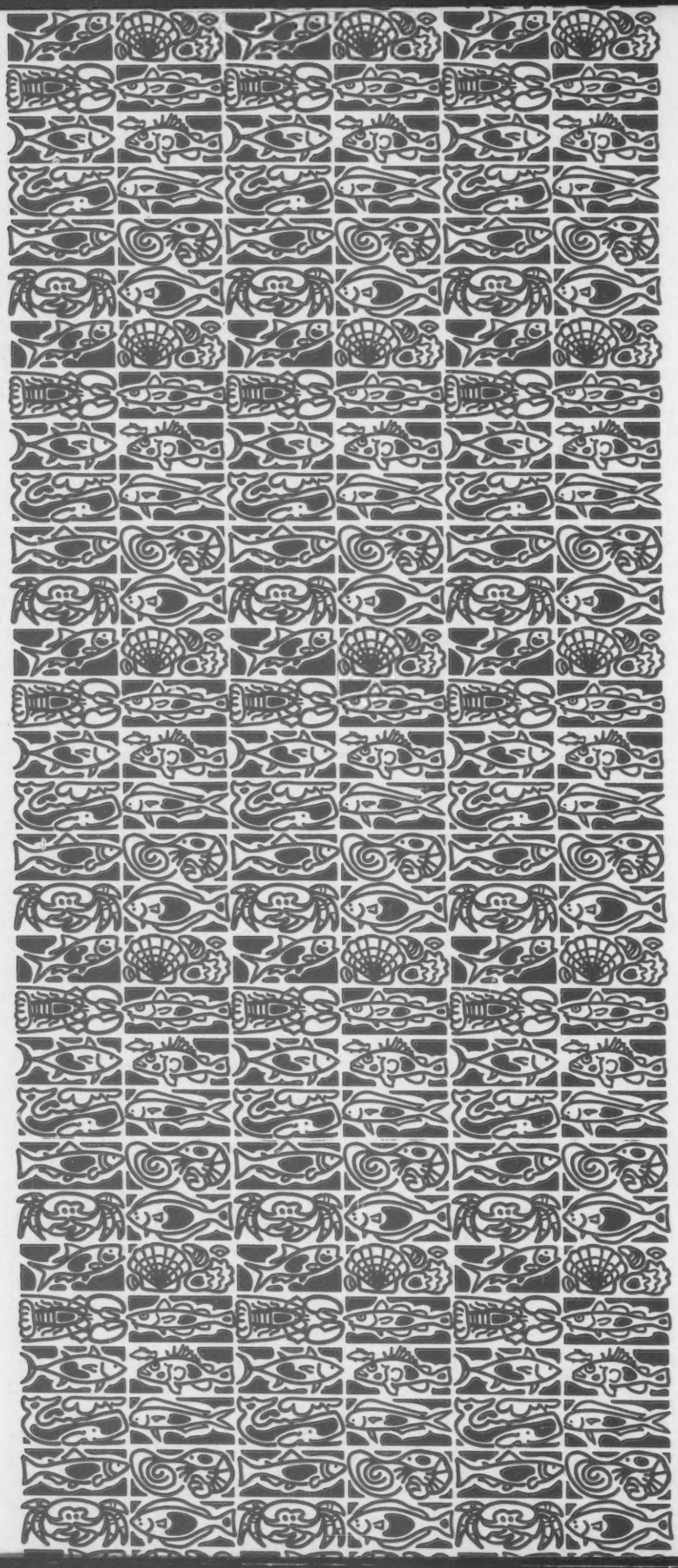

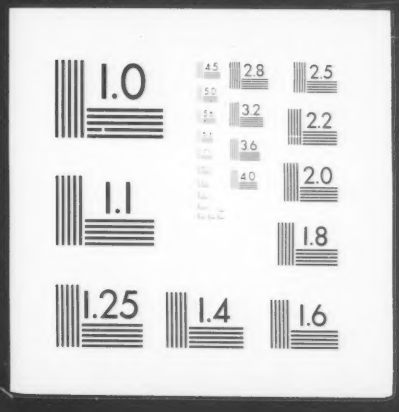
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